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T H E   U N I V E R S I T Y   O F   A L B E R T A

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                    Spermophilus parryii.

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'THESE MEN WERE NOT HIS RELATIVES AND THEY WERE THEREFORE  
HIS ENEMIES.'

A.R. Radcliffe-Brown, 1974  
In Cohen, Y.A., Man in  
Adaptation

The country beneath  
the earth has a green sun  
and the rivers flow backwards;

the trees and rocks are the same  
as they are here, but shifted.  
Those who live there are always hungry;

from them you can learn  
wisdom and great power,  
if you can descend and return safely.

Margaret Atwood  
(Procedures for Underground)



THE UNIVERSITY OF ALBERTA

Social Ecology of the Arctic ground squirrel

Spermophilus parryii

by



Ian Gordon McLean

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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THE UNIVERSITY OF ALBERTA  
FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Social Ecology of the Arctic ground squirrel Spermophilus parryii submitted by Ian Gordon McLean in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Zoology.





## ABSTRACT

Arctic ground squirrels (Spermophilus parryii plesius) were studied near Haines Junction, Yukon Territory, during the summers of 1977, 1978, and 1979.

The population was trapped weekly to obtain data on dispersal, patterns of weight change and wounding, and reproductive success. Juveniles were trapped as they emerged from natal burrows to ensure that kin relationships were known. Two areas were gridded in 15 x 15 m squares and all ground squirrels living in them were marked with individual dye patterns. Observations were conducted in these areas from platforms 2.5 m high. Positions, and activity at each position, of animals were sampled instantaneously to obtain data on home range and behaviour. Plant species taken as food were determined from monthly samples of feces collected during 1978. These were related to the abundance of plant species in areas in which ground squirrels were observed to feed.

Female arctic ground squirrels exhibited nepotism. Due to differential dispersal of males and females, only female kin were likely to live near to each other. Close female kin (sisters, mothers/daughters) had greater overlap of home ranges and interacted more amicably and less agonistically, than did less closely related females. Values for distant relatives (known genetic relatives that had not associated in a natal burrow) were intermediate (overlap of home ranges) to those for close and non-relatives, or were more similar to those of non-relatives (interactions, distances between natal burrows). I suggest that females benefit from associations with relatives during periods





that infanticide by males is likely.

Male arctic ground squirrels defended territories. Spatial separation and territorial defence were most obvious during the periods that females were giving birth and juveniles were underground. Male arctic ground squirrels committed infanticide. Infanticide was most likely in areas where the male that had been resident in an area during the mating period (and hence the likely father of young in that area) was removed. Males that moved in (unlikely fathers) tended to kill young. I suggest that territoriality by males prevents infanticide, and that males give paternal care as a consequence.

Arctic ground squirrels fed predominately on legumes (including the genera Oxytropis, Astragalus, Hedysarum, and Lupinus), and on sage (Artemisia). The low abundances of these in feeding areas indicated that ground squirrels fed selectively. The overall diets of males and females were very similar, but some differences between the sexes in the timing of changes in diet occurred.

In addition to showing some differences in feeding habits, male and female arctic ground squirrels adopted different tactics for the hibernation period. Males stored food and lost little weight through the winter. Females entered hibernation earlier and lost more weight than males. Males lost weight in the spring, whereas females did not. I suggest that these differences are related to the length of the mating period, which for males lasts for several weeks, whereas for females it lasts for one or two days.



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# TABLE OF CONTENTS

	PAGE
GENERAL INTRODUCTION	1
CHAPTER ONE      FEEDING ECOLOGY OF ARCTIC GROUND SQUIRRELS ( <u>Spermophilus parryii</u> <u>plesius</u> ) IN THE SOUTHWEST YUKON	4
Introduction	4
The Study Area	5
The Study Animal	8
Methods	9
Results	12
Discussion	18
CHAPTER TWO      THE ASSOCIATION OF FEMALE KIN IN THE ARCTIC GROUND SQUIRREL	22
Introduction	22
Methods	24
Study area and trapping program	24
Home range: estimates of size and overlap	25
Kin relationships and interactions	28
Results	29
Dispersal of arctic ground squirrels	29
Size and overlap of female home ranges through the season	33
Interactions between adult females	34
Distribution of natal burrows and family movements	38
Movements of emerged young	44





	PAGE
CHAPTER TWO, cont'd	
Discussion	47
Why did females clump their young?	47
The basis of nepotism among females	50
CHAPTER THREE      PATERNAL BEHAVIOUR AND INFANTICIDE IN ARCTIC GROUND SQUIRRELS	53
Introduction	53
Methods and Study Area	55
Trapping program	56
Home range and time budgets	57
Interactions	58
Dispersing and excursiioning by adult males	61
Experimental removal of adult males	62
Results	63
Wounding and interaction rates	63
Overlap of home ranges and parallel runs	69
Time budgets of male and female arctic ground squirrels	76
Dispersal and excursiioning by adult males	80
Infanticide: its perpetrators and occurrence	83
Infanticide: did the males eat their victims?	89
Infanticide: experimental removal of adult males	89
Discussion	92
Why do males defend territories?	93
Absence of males from their territories	97
Why did males commit infanticide?	99
Behaviour of females	104
Conclusion	105



SUMMARY AND CONCLUSIONS	107
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\*\*\*\*\*

BIBLIOGRAPHY	111
--------------	-----

APPENDIX 1. DIFFERENCES IN WEIGHT CHANGES AND THE ANNUAL CYCLE OF MALE AND FEMALE ARCTIC GROUND SQUIRRELS	118
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APPENDIX 2. WEIGHTS OF ARCTIC GROUND SQUIRRELS ON BEAR CREEK FLATS, YUKON TERRITORY, DURING 1977, 1978, AND 1979.	144
---	-----

APPENDIX 3. PLUGGING OF NEST BURROWS BY FEMALE <u>Spermophilus</u> <u>columbianus</u>	145
--	-----

APPENDIX 4. COPULATORY PLUGS IN GROUND SQUIRRELS	148
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## LIST OF TABLES

	Description	Page
 CHAPTER ONE		
Table 1	Percentage of food items identified by micro-histological analysis in the feces of adult male and female arctic ground squirrels from Bear Creek flats, Yukon Territory, during the active season in 1978.	13
2	Abundance of plant species in areas where feeding by arctic ground squirrels was common, and in areas where it was rare during two-weekly intervals in 1979	15
3	Comparison of plant species found in fecal samples, and therefore eaten by ground squirrels, and species found in feeding areas, and therefore likely to be eaten by ground squirrels	17
 CHAPTER TWO		
Table 1	Types of interaction observed between adult female arctic ground squirrels of each class of relationship during 1978 and 1979	37
2	Distances to nearest natal burrow of females of various classes of relationship during 1978 and 1979	43
 CHAPTER THREE		
Table 1	Categories of behaviour used in the field and for development of a time budget	59
2	Percentage of interactions between adult male arctic ground squirrels involving parallel runs during the mating period (15 - 30 April) and the period when juveniles were underground (14 May - 11 June) in 1978 and 1979	75
3	Differences in time budgets of male and female arctic ground squirrels during 1977, 1978, and 1979	79
4	Evidence for the ten instances of infanticide recorded and the history of the male perpetrators	84



	Description	Page
CHAPTER THREE, cont'd		
Table 5	Reproductive success of female arctic ground squirrels in control and experimental areas during 1978 and 1979	91





## LIST OF FIGURES

	PAGE
 CHAPTER ONE	
Figure 1     The study area on Bear Creek flats, Yukon Territory	7
 CHAPTER TWO	
Figure 1     Date of first capture of juvenile arctic ground squirrels	32
2        Percent overlap of home ranges of closely, distantly, and unrelated female arctic ground squirrels during 1978 and 1979	36
3        Distribution of natal burrows and movements of families of arctic ground squirrels on one observation area in 1979	41
 CHAPTER THREE	
Figure 1     Index of wounding of arctic ground squirrels during the active seasons of 1977, 1978, and 1979	65
2        Rates of interactions between males, and between male and female arctic ground squirrels during 1978 and 1979	68
3        Home range and interactions of a central male during two periods in 1979	71
4        Change of exclusiveness of male home ranges through the active season during 1978 and 1979	74
5        Time budget of male and female arctic ground squirrels in 1979	78
6        Dispersal and excursioneing by adult male arctic ground squirrels during 1977, 1978, and 1979	82



## GENERAL INTRODUCTION

Discussions of the evolution and maintenance of social behaviour usually incorporate defensability of resources (Brown, 1964; Brown and Orians, 1970) as a major factor governing the type of social system recognised (e.g. Wolf, 1978; Ewald and Carpenter, 1978; Murie and Harris, 1978; Pitelka et al., 1974). Animals which live in groups are usually assumed to have more efficient access to essential resources as a result of group living, than if they lived solitarily (Hoogland and Sherman, 1976). Such advantages may be indirect, for example if group living is an anti-predator strategy which frees individuals to utilise their resources without being constantly on the alert (Bertram, 1978), or direct, as in lekking species where males which attempt to breed solitarily likely achieve fewer copulations than those on the lek (Emlen and Oring, 1977). Recent interpretations of the evolution of social behaviour have invoked kin selection (Hamilton, 1964; West Eberhard, 1975, for a review) and reciprocal altruism (Trivers, 1971) as major factors governing the occurrence of group living and superficially unselfish ("altruistic") behaviour. Although some situations in which kin selection appears to be occurring may be better explained in terms of individual selfishness (Woelfenden and Fitzpatrick, 1978), it is hypothesised that individuals will selectively favour relatives if by so doing, they gain in inclusive fitness (Hamilton, 1964; Maynard Smith, 1964).

The social organisation of ground squirrels (Marmotinae) ranges from solitary living individuals to multi-harem colonies (Dunford, 1977a; Armitage, in prep., Michener, in prep.). Arctic ground squir-





rels (Spermophilus parryii) show an intermediate form of social system. Adult males are territorial, and appear to defend "harems" (Carl, 1971), but little or no intersexual grouping occurs within the colonies. Whether kin selection contributes to the maintenance of coloniality in ground squirrels is not known, although it is suspected (Dunford, 1977a, b; Sherman, 1977, 1980a; Armitage, in prep.). The pattern of dispersal (males disperse, females do not) found in many species suggests that spatial aggregation of female kin could occur. Females appear to recognise kin in S. richardsonii (Michener and Sheppard, 1972; Michener, 1974), S. tereticaudus (Dunford, 1977a), and S. beldingi (Sherman, 1980a). Recognition experiments are continuing in several species, including S. parryii (W.G. Holmes, Department of Psychology, University of Michigan, pers. comm.).

Infanticide appears to be prevalent in the Marmotinae, although only in S. beldingi has its documentation been more than anecdotal (Sherman, 1980b). Hibernating ground squirrels rarely breed more than once per year (Banfield, 1974), so that infanticidal attacks by conspecifics can greatly affect the reproductive success of individuals during a season. Infanticide has consequently been proposed as a major factor around which the social systems of several ground squirrel species are organised (McLean, 1978; Sherman, 1980b). Reports of its occurrence during field studies of arctic ground squirrels (Steiner, 1972) suggest that it may be important in this species.

Arctic ground squirrels are a member of a wide ranging group (the Sciuridae) which extend across five continents (Moore, 1961; Black, 1972). The species is of particular interest as the only



Holarctic member of the genus Spermophilus, extending across northern Canada, through Alaska, and into northeastern Siberia (Banfield, 1974). Evidence from chromosome number suggests that S. parryii evolved directly from S. richardsonii (Liapunova and Vorontsov, 1970), whereas evidence from biochemical studies related S. parryii more closely to the Palearctic S. undulatus, and to S. columbianus (Nadler, 1968; Nadler et al., 1975). Although some differences in life history traits have been noted (Murie et al., 1980), published data on these species suggests that the social organisation of S. parryii is most similar to that of S. columbianus (Armitage, in prep.).

This study was designed to investigate the social system of arctic ground squirrels, with particular emphasis being placed on the association of kin, and the occurrence of infanticide. The thesis is organised in three chapters, plus appendices; specific questions and hypotheses are formulated in each chapter. The chapters, and Appendix one, have been written as separate and independent papers, with the exception that some cross referencing to methodology has been made to avoid repetition. In Chapter one, I describe the study area, and the feeding ecology of arctic ground squirrels. In Chapter two, I describe the pattern of dispersal and the association of female kin. In Chapter three, I describe the social system of males and the occurrence of infanticide.





## CHAPTER ONE

### FEEDING ECOLOGY OF ARCTIC GROUND SQUIRRELS

(Spermophilus parryii plesius)

IN THE SOUTHWEST YUKON

#### INTRODUCTION

Ground squirrels (genus Spermophilus) are known to take a wide variety of foods, including green vegetation, seeds, invertebrates, dead animal material, and small vertebrates, including members of their own species (Hisaw and Emergy, 1927; Hansen and Ueckert, 1970; Hansen and Johnson, 1976; Slade and Balph, 1974; Gordon, 1943; Johnson, 1977; Sherman, 1980b). Where enough information was obtained, the general consensus from these studies was i) that there were few differences in diet between males and females, and ii) that the diet changed through the season of activity. A common pattern was use of green vegetation early in the season with some switching to seeds and/or invertebrates as the season progressed. Apart from anecdotal reports of food hoarding (Mayer, 1953; Krog, 1954; Appendix 1), little is known of the food habits of the arctic ground squirrel (Spermophilus parryii). In this study I monitored the foods taken by male and female S. parryii plesius in the southwestern Yukon through the active season, and the areas within the study area in which ground squirrels fed. These data allowed me to relate the diet to the availability of food species, and hence provide a preliminary assessment of whether arctic ground squirrels feed selectively.



## THE STUDY AREA

The study area, called Bear Creek flats, was located ten kilometres west of Haines Junction, Yukon Territory, at the entrance to the Alsek River Valley ( $67^{\circ}47'N$ ;  $137^{\circ}40'W$ , elevation 600 m) (Fig. 1). It consisted of meadows within extensive areas of willow (primarily Salix glauca) and was bounded by Bear Creek on the north and west sides, spruce forest (Picea mariana) to the west, and other meadows and a second small creek to the south. Stands of aspen (Populus tremuloides) occurred throughout the area. Soils in the meadows, where most ground squirrels lived, had a high gravel content and were well drained. Plant species found commonly in the meadows included Artemisia frigida, Erigeron compositus, Penstemon gormanii, Oxytropis campestris, Anemone sp., Carex supina, and various grasses. Hedysarum boreale was locally abundant along meadow/willow interfaces. Several Astragalus spp. grew in the willows. A detailed analysis of the vegetation in the general area was presented by Douglas (1974) and the physiography was described by Oswald and Senyk (1977).

Weather in the summer was dry and windy. Some hot periods (up to  $28^{\circ}C$ ) occurred in July and August, but frosts were recorded in every month. Mean temperature in July (the hottest month) is  $12^{\circ}C$  (Haines Junction records). Most rain fell in late May, early June, and early July in 1977 and 1979. A drought occurred from snowmelt in April until mid August in 1978, and most vegetation dried up by mid July. Rainfall in the area in 1977 and 1978 is given in Appendix 1. Snow cover through the 1977/78 and 1978/79 winters was approximately







Figure 1: The study area on Bear Creek flats, Yukon Territory.

Area of detailed study (control area) is outlined in dots. Observation meadows are marked A and B. Positions of observation platforms are indicated with large dots.

The area designated R was the 1979 experimental (removal) area. The 1978 experimental area was 10 km to the south (see Chapter 3).

The town of Haines Junction is 10 km to the east. The Alaska Highway runs parallel to the pipeline off the north end of the map.





one metre from December through March. All snow had melted by mid-April in 1977 and by early May in 1978 and 1979.

The study area was visited from 28 April through 15 October, 1977, 15 April through 27 September, 1978, and 2 April through 8 July, 1979. I was never absent for more than four consecutive days during these periods.

#### THE STUDY ANIMAL

The following summary of the ecology of S. parryii plesius is taken from Green (1977) and from my unpublished data (see also Appendices 1 and 2). Green worked on two populations at elevations of 800 and 1525 m in an area 60 kilometres northwest of my study area from April 1975 until June 1977. I trapped ground squirrels on Green's high altitude site once weekly through 1977 until they entered hibernation.

Arctic ground squirrels in the southwest Yukon were active from mid April through October. Mating occurred from emergence of females until early May, females gave birth from mid-May until early June, and juveniles emerged between mid-June and early July. The timing of seasonal events varied slightly with elevation, with animals at higher elevations emerging later from hibernation, and events such as births, etc., were consequently delayed. Males emerged from hibernation before females and entered hibernation up to two months later (these differences were smaller at higher elevations). Males estab-





lished stores of seeds in the autumn whereas females did not (not found by Green), and males lost less weight than females through the winter. Females were more abundant in the population, although large sample sizes were required for this difference to be statistically significant. The sex ratio at birth was near unity and males may have suffered a higher mortality during dispersal. Females remained near their natal areas. Males usually weighed about 15% more than females, although this varied from 0% to 25% depending on the stage of the season and the year. The biggest differences in the weight of males and females occurred in the early spring, and in late June when juveniles were emerging. Both sexes bred as yearlings. Males defended territories during most of the active season. Home ranges of females were smaller than those of males, but females did not always restrict their activities to the territory of only one male.

#### METHODS

Most animals in the study population were live-trapped each week as part of studies on demography and behaviour. All trapping occurred during the morning; thus animals were able to feed for up to several hours before being captured. Beginning with the week 17 - 23 April, fecal material was collected from all adult ground squirrels captured every second week during 1978. Three large or four small pellets were taken from each animal; it was very rare for an animal not to produce this amount during handling. Pellets



were kept separate by sex, air dried, and each pair of successive biweekly collections were combined to give monthly samples. Each sample therefore consisted of pellets taken from most male or female adult ground squirrels in the population during a monthly period. A variable number of animals were represented twice in the sample. Six samples for males and five for females (too few females were captured in September for an adequate sample to be obtained) were sent to the Composition Analysis Laboratory, Colorado State University, Fort Collins, Co. 80523, for analysis.

Details of methodology for the microhistological analysis of feces to determine herbivore diets are in Hansen, et. al. (unpubl. manus.) which is available on request from the Composition Analysis Laboratory. Briefly, each sample of fecal material was subsampled to obtain 20 histological slides of finely ground material. Twenty fields on each slide were viewed at 100x magnification and the plant fragments identified by reference to slides prepared from species known to occur in the area. A total of 400 fields per sample were viewed. The percent frequency of occurrence of each species in the diet was calculated by dividing the number of fragments of that species by the total number of identified fragments and multiplying by 100.

The areas in which ground squirrels fed were determined by mapping all points at which animals were observed feeding. Behaviour and position of individually marked animals were sampled with reference to a 15 x 15 m grid by making daily observations from 2.5 m high towers. Each animal was sampled instantaneously (see Altmann, 1974) as it was encountered during a scan of the observation area. Details of methods



and the results obtained are presented elsewhere (Chapters 2 and 3).

To compare the plant species found in areas where animals spent most time feeding, with those in areas where little feeding occurred, I drew transects by eye across maps of feeding observations from each two week interval of the preceding active season. For example, transects sampled in mid May, 1979, were based on maps of observations of animals feeding during the first two weeks of May, 1978. These transects were located in the field using the grid system and plant species were sampled by noting the nearest plant to each 20 cm point along a 10 m line. Mosses or lichens were noted if no other plant occurred in a 5 cm radius around the point. Bare ground was noted if no mosses or lichens were present.

Five transects were run through areas where feeding by ground squirrels was common ("feeding" areas), and five were run through areas where feeding was rare ("non-feeding" areas) after each two week interval beginning 16 - 29 April, 1979. Samples were taken for three sets of two week intervals termed late April, early May, and late May for a total of 30 transects and 1500 samples for each of feeding and non-feeding areas. A total occurrence of each plant species in feeding and non-feeding areas was calculated for each two week period, and these were summed to give an overall total. The abundance of plant species in each area were compared using the Wilcoxon test for matched pairs. Differences were considered not significant if the probability level was greater than 0.1. Probability levels less than 0.1 are indicated in the text.





## RESULTS

Legumes were the major plant group consumed by arctic ground squirrels during 1978 (Table 1). This group, including the genera Astragalus, Oxytropis, and Hedysarum, were not distinguishable using microhistological analysis. Grasses were not a major component of the diet, although Deschampsia formed slightly more than 10% of the diet in the spring. Other genera forming more than 10% of the diet during some periods included Antennaria in the spring and again for males in September, Salix in June, Lupinus in July and August, and Artemisia in the fall. Ground squirrels spent long periods climbing in Salix bushes in June in all years and were taking developing catkins and leaf buds. The peak in Lupinus in July and August coincides with the period when this species was seeding, and several cheek pouch collections taken from males included Lupinus seeds. However, although no attempt was made to quantify the relative proportions of materials from various parts of the plant, there was no qualitative indication of a major shift in the diet to seeds (T.M. Foppe, Composition Analysis Laboratory, pers. comm.).

The only period during which legumes did not form the major component of the diet was the autumn, when both sexes switched to Artemisia. However, males switched a month later than females, with the result that the diet of each sex was considerably different in August. Some Antennaria was also consumed after this switch, more so by males than by females. Males also took Anemone in September. The diets of both sexes were very similar before August. Arthropods did not form a



Table 1: Percent frequency of food items identified by microhistological analysis in the feces of adult male and female arctic ground squirrels from Bear Creek flats, Yukon Territory, during the active season in 1978.

	April 17-23 May 1-7	May 15-21 May 29-Jun 4	June 12-18 June 24-30	July 10-16 July 24-30	August 7-13 August 21-27	Sept. 4-10 Sept. 18-24	Total						
	*M:29 F:39	M:47 F:91	M:45 F:105	M:58 F:60	M:40 F:25	M:31	M:250 F:320						
Grasses, total	11.52	13.82	3.72	7.07	.98	.70	3.31	5.28	.09	2.23	2.22	3.64	5.82
<u>Deschampsia</u>	10.75	13.55	2.85	6.00	.21	.58	-	-	.05	2.17	2.19	2.68	4.46
Grass, unident.	.12	-	.03	-	-	-	1.50	3.58	-	-	-	.28	.72
<u>Poa</u>	.53	-	-	-	.62	-	1.67	1.33	-	.03	-	.47	.27
<u>Festuca</u>	.12	.27	.84	1.07	.15	.06	-	.07	-	.03	.03	.19	.30
<u>Calamagrostis</u>	-	-	-	-	-	.06	.14	.30	-	-	-	.02	.07
<u>Hierochloe</u>	-	-	-	-	-	-	-	-	.02	-	-	.00	.00
<u>Agropyron</u>	-	-	-	-	-	-	-	-	.02	-	-	.00	.00
<u>Carex</u>	-	.15	1.18	1.86	.09	.20	.17	-	-	.11	.03	.25	3.43
Legumes <sup>+</sup>	79.88	82.07	72.72	74.76	84.32	78.97	66.84	68.22	63.96	8.22	2.52	61.71	62.45
<u>Artemisia</u>	.29	.57	.34	.13	.43	.08	.39	.35	13.53	73.01	73.91	14.82	14.83
<u>Lupinus</u>	.59	-	5.09	3.69	.235	7.16	27.69	25.58	21.75	7.23	1.14	9.77	8.73
<u>Antennaria</u>	5.50	2.88	12.77	9.39	1.57	1.97	-	-	-	5.82	11.79	5.27	4.01
<u>Salix</u>	.14	-	3.82	2.72	9.68	10.20	1.17	.25	.05	.03	-	2.48	2.64
<u>Anemone</u>	-	-	-	-	-	-	-	-	-	-	6.41	1.07	.00
Compositae unident.	.83	.33	.08	.11	.40	.43	.39	.30	.52	2.53	1.17	.57	.74
<u>Potentilla</u>	1.08	.15	-	.08	.03	-	-	-	.05	.11	.60	.29	.07
<u>Descurainaea</u>	.14	-	.05	-	.06	.03	-	-	-	-	.11	.06	.00
<u>Shepherdia</u>	-	-	.10	-	.06	-	.02	-	-	.03	-	.03	.01
<u>Achillea</u>	-	-	.08	.08	-	.03	-	-	-	-	-	.01	.02
<u>Rosa</u>	.03	.03	-	-	-	-	-	-	-	-	.05	.01	.01
<u>Equisetum</u>	-	-	-	.03	.03	-	-	-	-	.03	-	.00	.01
<u>Rubus</u>	-	-	-	-	-	-	-	.02	.05	-	-	.01	.00
Moss	-	-	-	.03	-	-	-	-	-	-	-	.00	.01
Arthropoda	-	-	.05	.05	-	.23	.02	-	-	.65	.05	.02	.19

\* M = male, F = female. Number after the letter gives the number of ground squirrels from which fecal pellets were taken.

<sup>+</sup> Includes genera Oxytropis, Hedysarum, Astragalus.





major component of the diet at any time.

Carex supina was the most abundant plant found in both feeding and non-feeding areas, followed closely by grasses (Table 2). Erigeron compositus was the next most abundant, followed by Artemisia frigida and Penstemon gormanii. Except for the grass Deschampsia, none of these species formed major components of the diet (Table 1) during the sampling period. The legumes found in these areas (Oxytropis, Hedysarum, Astragalus) were uncommon, and there was little difference in their abundance between areas. Sage (Artemisia frigida) was twice as common in feeding as in non-feeding areas, but no data are available on whether ground squirrels fed in the same areas in the autumn, when sage formed a major component of the diet, as in the spring, when it did not. The number of species found in each area was similar.

No significant differences were found between i) the abundance of plant species in feeding areas in the two observation areas, or ii) the abundance of plant species in different feeding areas during any of the three periods sampled, so these sets of data were combined. Similar results were obtained for non-feeding areas, and these data were also combined. No significant differences were found in the abundance of plant species in feeding and non-feeding areas during any period, nor were all data combined (last columns in Table 2) significantly different.

I compared the occurrence in transects through feeding areas with the occurrence in transects through non-feeding areas (N = 30 for each type of area) of the five most abundant species (or species



Table 2: Abundance of plant species in areas where feeding by arctic ground squirrels was common, and in areas where it was rare during two weekly intervals in 1979. Data are based on transects run through maps of feeding distributions obtained in 1978.

	Late April		Early May		Late May		Total	
	*NF	F	NF	F	NF	F	NF	F
<u>Carex supina</u>	115	168	170	140	134	135	419	443
Grasses	126	101	101	139	93	131	320	371
<u>Erigeron compositus</u>	72	60	75	38	98	63	245	161
<u>Artemisia frigida</u>	23	46	12	35	16	19	51	100
<u>Penstemon gormanii</u>	37	30	24	39	31	29	92	98
<u>Anemone sp.</u>	8	16	10	11	9	11	27	38
<u>Saxifraga tricuspidata</u>	14	0	7	10	11	20	32	30
<u>Potentilla pennsylvanica</u>	13	9	8	10	10	8	31	27
<u>Chamaerhodos erecta</u>	10	0	6	3	7	8	23	11
<u>Oxytropis campestris</u>	6	9	4	2	0	2	10	13
<u>Solidago spathulata</u>	9	3	2	4	0	2	11	9
<u>Cruciferae (unident.)</u>	2	2	1	1	4	5	7	8
<u>Antennaria umbrinella</u>	0	1	2	1	2	1	4	3
<u>Salix glauca</u>	1	0	1	0	0	0	2	0
<u>Hedysarum boreale</u> var. <u>mckenzie</u>	0	0	1	3	3	0	4	3
<u>Ranunculus sp.</u>	0	0	1	0	0	0	1	0
<u>Sedum sp.</u>	0	0	1	0	0	1	1	1
<u>Androsace septentrionalis</u>	0	0	0	1	0	0	0	1
<u>Galium boreale</u>	0	0	0	1	0	0	0	1
<u>Astragalus sp.</u>	0	0	0	0	2	0	2	0
<u>Achillea millefolium</u>	0	0	0	0	0	1	0	1
<u>Linum perenne</u> var. <u>lewisii</u>	0	0	0	0	0	1	0	1
Lichen/moss	25	11	2	10	24	22	51	43
Unknown	0	3	3	4	3	10	6	17
Bare ground	39	41	69	48	53	31	161	120

\* NF = transects run through areas in which little or no feeding occurred  
F = transects run through areas in which most feeding occurred  
Numbers represent total counts for each species from a total of 1500 sampling points in 30 transects for each type of area.  
Species names follow Douglas (1974).



groups) using a Mann Whitney U test. No significant differences were found; for example Erigeron compositus did not occur significantly more in transects through non-feeding areas than through feeding areas, as is suggested by inspection of the data.

To test the hypothesis that arctic ground squirrels fed randomly on those plant species found in feeding areas, I compared the proportions of plant species actually eaten during April, May, and early June (I took a mean percent of the first four columns in Table 1) with the abundance of plant species in feeding areas (last column in Table 2) using Spearman's rank correlation coefficient (Table 3). Species were only included in this analysis if i) they occurred more than once in feeding areas if absent from fecal samples, or ii) they occurred in both fecal samples and in feeding areas. These criteria excluded Salix, Lupinus, Equisetum, Rosa, Rubus, and Sheperdia, which although consumed by ground squirrels and common in parts of the study area, were not found in the feeding areas.

No correlation was found between the abundance of plant species in feeding areas and the species consumed by ground squirrels ( $r_s = 0.21$ ,  $P > 0.1$ , Table 3), indicating that ground squirrels did not feed randomly on those species found in feeding areas.

Since the abundance of plant species in feeding areas was similar to their abundance in non-feeding areas, I tested the hypothesis that proximity of burrows determined where ground squirrels fed by measuring the distance to the nearest burrow system from each end of the 60 transect lines sampled. Mean ( $\pm$  s.e.) distance to the nearest burrow





Table 3. Comparison of plant species found in fecal samples, and therefore eaten by ground squirrels, and species found in feeding areas, and therefore likely to be eaten by ground squirrels (taken from columns one through four, Table 1, and the last column, Table 2).

	Found in fecal samples (%)	Found in feeding areas (abundance)
<u>Carex</u>	0.80	443
Grasses	9.03	371
<u>Erigeron</u> + <u>Solidago</u> *	0.34	170
<u>Artemisia</u>	0.33	100
<u>Penstemon</u>	0	98
<u>Anemone</u>	0	38
<u>Saxifraga</u>	0	30
<u>Potentilla</u>	0.33	27
Legumes	77.36	16
<u>Chamaerhodos</u>	0	11
Cruciferae	0.05	8
<u>Antennaria</u>	7.64	3
<u>Achillea</u>	0.04	1

\* Frequency of occurrence of unidentified Compositae in Table 1 used to pair with Erigeron and Solidago in feeding areas as squirrels were observed to feed on these species but they were not identified in fecal analysis.

Species were only included in this analysis if:

- i) they occurred more than once in feeding areas if absent from fecal samples;
- ii) they occurred in both fecal samples and in feeding areas.



for transects through feeding areas was  $4.5 \pm 0.49$  m ( $N = 60$ ), and through non-feeding areas was  $10.6 \pm 0.76$  m. This difference was significant ( $t$  test,  $P < 0.05$ ) indicating that animals were more likely to feed where there was a burrow nearby.

#### DISCUSSION

Legumes formed approximately 70% of the diet of male and female arctic ground squirrels on Bear Creek flats, Yukon Territory, during 1978. Sage (Artemisia frigida) formed another 15%; thus a small number of species made up approximately 85% of the diet. Except for sage, which was consumed in quantity only in the autumn, these plant species were not common in the study area. The data therefore indicate that arctic ground squirrels were selective when taking plant species as food. They were also selective when choosing foraging areas within the meadows, although I found no indication that this was related to the plant species available in those areas. Rather, feeding occurred where burrow systems were available nearby, presumably because burrow systems represent an avenue of escape from predators.

Two assumptions implicit in the analysis presented here are i) that fecal samples collected from animals that had previously fed for several hours during the early morning are representative of foods taken during all parts of the day, and ii) that dietary components determined from those samples could be related to the areas in which ground squirrels were observed to feed during the morning. Although



most activity of ground squirrels in the morning, including that of feeding, took place in the meadows, fecal samples taken during the morning could reflect foods eaten the previous afternoon. Some animals moved out of the meadows during hotter parts of the day, and some feeding probably occurred in areas of willow where observations could not be made, and where some different plant species to those in the meadows were available. I have no data on the proportion of feeding that occurred outside the meadows, nor can I assess the validity of either of the assumptions. The following discussion must be considered with these limitations in mind.

The microhistological technique did not allow differentiation among the legumes Oxytropis, which was most common in the meadows, and Astragalus and Hedysarum, which were more common in areas that were out of view. Oxytropis plants were heavily grazed during the spring but became leafy in late June, indicating that they had overcome grazing pressures. Moose (Alces alces), porcupine (Erethizon dorsatum), hares (Lepus americanus), and feral horses were all seen grazing on Oxytropis during this study, and ground squirrels were also observed feeding on Oxytropis plants for long periods in patches where they were abundant. It was likely that some competition for food occurred between ground squirrels and other mammals.

More feeding by ground squirrels in the vicinity of burrow systems suggests i) that preferred plant species were more available near burrows, or ii) that more food was available than was being consumed, or iii) that benefits derived from remaining near to burrow systems were greater than those derived from obtaining preferred foods further





away. The activities of some ground squirrel species modifies vegetation characteristics and may encourage the growth of preferred plant species (King, 1955; Kozhemyakin, 1978). However, semi-fossorial mammals will feed as near to burrows as the distribution of food species allows (Marmota caligata, Holmes, 1979; Oryctolagus cuniculus, Gibb et. al., 1978). My data on the abundance of plant species in feeding and non-feeding areas did not indicate that preferred plant species were more available near to burrows, but more data are needed on all these aspects before definite conclusions can be drawn.

The switch by male and female arctic ground squirrels to Artemisia in the autumn suggests either that Artemisia provides nutritive substances, such as carbohydrates or fats, that are presumably required for hibernation, or that other plant species became unavailable or poor in quality as the season progressed. This result was complicated by 1978 being an unusually dry year. Artemisia is adapted to dry conditions in this area (Douglas, 1974) and may have been the only food source available in abundance in that year. Herbaceous plants do tend to decrease in quality in the autumn (Scotter, 1972), but I have no data on whether Artemisia is less likely than other plant species to do so. The later switch from legumes to Artemisia by males suggests that females switched when legumes were still available. Females entered hibernation before males, so the hypothesis that ground squirrels derived some benefit for hibernation may provide the more likely explanation.

In general, the data presented here suggest that the diet of arctic ground squirrels is restricted to a relatively small number of



plant species which are taken selectively. However, care must be taken when generalising from these data, since arctic ground squirrels are known to occur in a wide variety of habitats (Banfield, 1974; pers. obs.), in at least some of which (e.g. grasslands) sage and legumes may be rare or absent. Although the overall diet was very similar for males and females, differences in the timing of dietary changes found here suggest that investigations of dietary components and nutritive requirements of ground squirrels must allow for differences in the behaviour of subclasses of individuals.



## CHAPTER 2

### THE ASSOCIATION OF FEMALE KIN IN THE ARCTIC GROUND SQUIRREL

#### INTRODUCTION

Organisms that live in groups are usually assumed to have more efficient access to essential resources as a result of group living than if they lived solitarily (Hoogland and Sherman, 1976). Such advantages may be indirect, for example if group living is an anti-predator strategy which frees individuals to utilise their resources without being constantly on the alert for predators (Murton, et al., 1966; Bertram, 1978), or direct, as in lekking species in which males that attempt to breed solitarily achieve fewer copulations than those on the lek (Wiley, 1974; Emlen and Oring, 1977). Recent interpretations of the evolution of social behaviour have incorporated kin selection (Hamilton, 1963, 1964; West Eberhard, 1975) and reciprocal altruism (Trivers, 1971) as factors governing the occurrence of group living and superficially unselfish ("altruistic") behaviour (Wilson, 1975). Although stable social groups of unrelated individuals certainly occur (McCracken and Bradbury, 1977), it may be hypothesised that kin selection is operating wherever: i) closely related individuals that are capable of communicating tend to live nearer to each other than is the average for the population; or ii) where they do not live closer, closely related individuals have the capability of interacting selectively.

Kin selection "explains how aid that is self sacrificing ... can





evolve if sufficiently beneficial to relatives" (West Eberhard, 1975, p. 1). It differs from reciprocal altruism by being restricted to related individuals, and forms that part of an animal's "inclusive fitness" (Hamilton, 1964; Maynard Smith, 1964) resulting from indirect reproduction of its genes. Relatives need not be recognised, or recognisable, although this may be the case (Wu, et. al., 1980), and may facilitate the rate at which kin selection occurs (Sherman, 1980a). Nor is it necessary that unrelated individuals be discriminated against (Williams, 1966), although it may be hypothesised that kin selection will either be a secondary effect of reciprocal altruism, or will not occur, if non-relatives benefit at the same rate as relatives. Demonstration that kin selection is occurring requires long term studies in which individuals that benefit from aid given by relatives have a greater proportion of young than those that reproduce without aid in subsequent (preferably distant) generations (adapted from Thoday, 1958; see also Brandon, 1978). The implications of the term kin selection are conveniently avoided by referring to those behaviours which indicate that individuals selectively favour relatives as nepotism (Sherman, 1977, 1980a).

In the genus Spermophilus, related individuals are known to live in close proximity in at least five species (Dunford, 1977a; Slade and Balph, 1974; Sherman, 1977, 1980a; Michener and Michener, 1977; Murie, pers. comm.). In all species studied, differential dispersal of males and females resulted in only females living amongst relatives (this may not always be the case for S. richardsonii, Michener and Michener, 1973; or S. columbianus, Murie, pers. comm.). That nepotism may occur



has been shown for S. beldingi (Sherman, 1980a), S. tereticaudus, (Dunford, 1977a, b), and possibly S. parryii (Green, 1977). Recognition of kin by females has been shown for S. richardsonii (Michener and Sheppard, 1972; Michener, 1974) and is likely for S. beldingi (Sherman, 1980a). In this study I monitored the pattern of dispersal, the spatial distribution of animals of known relationship, and the interactions occurring amongst animals of known relationship, in a sub-arctic population of the Arctic ground squirrel (S. parryii plesius). These animals are conspicuous, diurnal, and colonial, and males defend territories and commit infanticide (Chapter 3). I hypothesised that related female arctic ground squirrels would live near to each other whereas related males would not, and that females would exhibit nepotism.

## METHODS

### Study area and trapping program

Arctic ground squirrels were studied at an elevation of 600 m on a 60 hectare area ten kilometres west of Haines Junction, Yukon Territory (61°47'N; 137°40'W). The study area, described in detail elsewhere (Chapter 1), consisted of meadows interspersed amongst areas of willow (predominantly Salix glauca), with scattered stands of aspen (Populus tremuloides) and spruce (Picea mariana). It was bounded to the north and east by Bear Creek, spruce forest to the west, and



meadows and willows to the south. Two meadows two to three hectares in size and 750 m apart were gridded in 15 m squares for detailed observations of behaviour.

Live traps (National or Tomahawk box traps baited with peanut butter) were set through the entire area once weekly and most animals in the population were captured at least once every two weeks. Details of the trapping procedure, including those related to sampling of dispersing animals, are given in Chapter 3. Juveniles were trapped as they emerged from the natal burrows in 1977 and 1978. Genetic relationships were known for most adults (animals one year and older) resident in the observation areas in 1978 and 1979. Animals whose genetic relationship was not known were left out of analyses involving degree of relationship.

On being captured, animals were tagged in both ears with individually numbered fingerling fish tags, and sex, weight, wounds and reproductive condition were noted. Animals in the observation areas were dyed with unique marks using "Clairol" blue/black human hair dye, or "Jamar D" (Nyanza Co.). Observations were conducted from stands 2.5 m high. We found that animals soon grew accustomed to the presence of an observer above ground level.

#### Home range: estimates of size and overlap

Position, and activity at that position, of all animals visible in the observation areas were sampled by scanning with binoculars (Bushnell 10 x 50) from one side to the other at a constant time interval. Data were noted for the instant at which the animal was encountered. Interactions were noted as they occurred and the "scan" was





continued from the point at which it stopped when the interaction began. Sampling intervals varied between five and thirty minutes as a result of differing densities of ground squirrels between observation areas and years.

Estimates of home range were obtained by the minimum polygon method (Hayne, 1949). All positions at which an animal was seen during each two week interval were plotted and connected according to the criteria:

- 1) Points more than 20 m from any other point were rejected as "excursions" unless a line connecting two other points passed within 20 m of that point.
- 2) Lines were drawn only if they were within 20 m of at least one point along their length. Where three or more points within 20 m of each other occurred in an area that was more than 40 m from all other points for the animal, these were connected as a separate home range.
- 3) A minimum of nine sightings within a two week period were required for a home range to be drawn.

The 20 and 40 m distances and minimum number of sightings were chosen after inspection of the data. Large variations in home range size occurred for animals with similar numbers of observations, so that criteria for including points based on some proportion of home range size (e.g. one third the distance between outermost points) tended to accentuate this variation. Home range estimates for many animals in each two week interval were based on greater than 50 points, so that exclusion of outermost points that affected size and overlap by relatively large amounts seemed warranted.



For most animals, the above criteria excluded no more than five sightings.

Home range sizes were calculated by laying a grid (7 x 7 m) over the polygon and counting the number of squares included. Percent overlap of home ranges was calculated from the formula:

$$\% \text{ overlap} = \frac{\text{number of squares in overlap region of animals A and B}}{\text{total number of squares used by both A and B}} \times 100$$

A zero value for overlap of neighbouring animals was included in the analysis if:

- 1) Their home ranges came to within 15 m of each other at some point and no third animal overlapped with both ranges at that point.
- 2) Their home ranges came to within 5 m of each other at some point if a third animal overlapped with both animals at all points where the home ranges were within 15 m. This criterion assumes that the third animal would act as a buffer to overlap of the two neighbouring but non-overlapping animals.

Animals whose home ranges did not come within the above criteria were not considered to be neighbours.

Absolute estimates of the sizes of home ranges were not obtainable during this study as all animals spent at least part of their time outside the observation meadows in areas of dense willow. In general, home ranges tended to be larger when densities were lower. I present data on percentage overlap of home ranges on the assumption that overlap was similar in meadow and willow.



### Kin relationships and interactions

Kinship was determined matrilineally as it was not possible to determine whether one or several males fathered a litter, nor to unambiguously assign a particular male as the father. Three classes of related animals were recognised:

- 1) Closely related. This included mother/offspring, and siblings within a litter.
- 2) Distantly related. This included half siblings (same mother in different years), cousins, aunts, grandmothers, and second cousins.
- 3) Unrelated. This included any animals not included in 1) and 2).

Interactions between females were classified as agonistic, amicable, or identification. Agonistic interactions included those in which a fight or chase occurred, and situations where one animal approached another and displayed any of several postures, including arching or flattening of the body, arching and flaring of the tail, short charges, and vocalisations (see Watton and Keenleyside, 1973). Unless a chase occurred it was not usually possible to assign an animal as having "won" or "lost" an interaction.

Amicable interactions included situations in which animals touched noses or mouths, as in "kissing" (Steiner, 1975), sniffed each other (the animals often sat or fed close together after the interaction), and allogroomed.

Identification interactions included those in which one animal approached another, sometimes by charging, but after a quick sniff with





or without contact, either animal would move away without any obvious continuation of the interaction. My observations indicated that arctic ground squirrels either had difficulty identifying other squirrels at a distance, or responded too rapidly to the presence of a newly sighted animal to allow identification. These interactions were most common between animals with overlapping home ranges and as they were not obviously amicable or agonistic in outcome, the more neutral "identification" term was applied.

## RESULTS

A total of 785 arctic ground squirrels were captured 5625 times during the periods 28 April through 15 October, 1977, 16 April through 26 September, 1978, and 7 April through 8 July, 1979. Of these, 397 were males and 388 were females; 309 males and 280 females were first captured as juveniles.

### Dispersal of arctic ground squirrels

The natal areas were known for 235 juvenile male and 245 juvenile female arctic ground squirrels captured in 1977 and 1978. Of these, three males (1.3%) and 102 females (41.6%) were resident less than 200 m from their natal areas in June of the following year. Of the 40 females tagged as juveniles in 1977 and resident less than 200 m from their natal areas in 1978, 27 were still resident less than 200 m from their natal areas in June, 1979. The other 13 had disappeared. Only one male tagged as a juvenile in 1977 was resident less than 200 m



from his natal area in 1979. This male had dispersed a relatively small distance (250 m) as a juvenile, and moved back towards his natal area in the spring of his second year.

No females, either juvenile or adult, moved large distances and established residence (defined here as being captured at least twice in the same area during any four week interval) in a new area during this study. The greatest movements recorded were by two juvenile females that resided as yearlings 200 and 210 m from their natal burrows. At this distance, they would be unlikely to interact with the female resident on their natal areas. Three adult and six juvenile females that did not return to their usual or natal areas were captured once at distances ranging from 230 to 690 m away. These females may have been dispersing.

Thirty five juvenile males dispersed and established residence 200 m or more from their natal areas before June of their yearling year during this study. Mean distance dispersed was  $554 \pm \text{s.e. } 52.2 \text{ m}$  (range 200 to 1400 m). These 35 represent 15% of the 235 juvenile males whose natal area was known, and 92% of the 38 males whose area of residence was known in June of their yearling year. An additional 13 males were captured once more than 200 m from their natal areas before June of their yearling year, but they were not subsequently recaptured.

To further investigate dispersal by juvenile arctic ground squirrels, I monitored the sex ratios of juveniles entering the population (Fig. 1). These animals came either from litters born on the study area, or by immigration from other areas. Juveniles began emerging in mid-June,

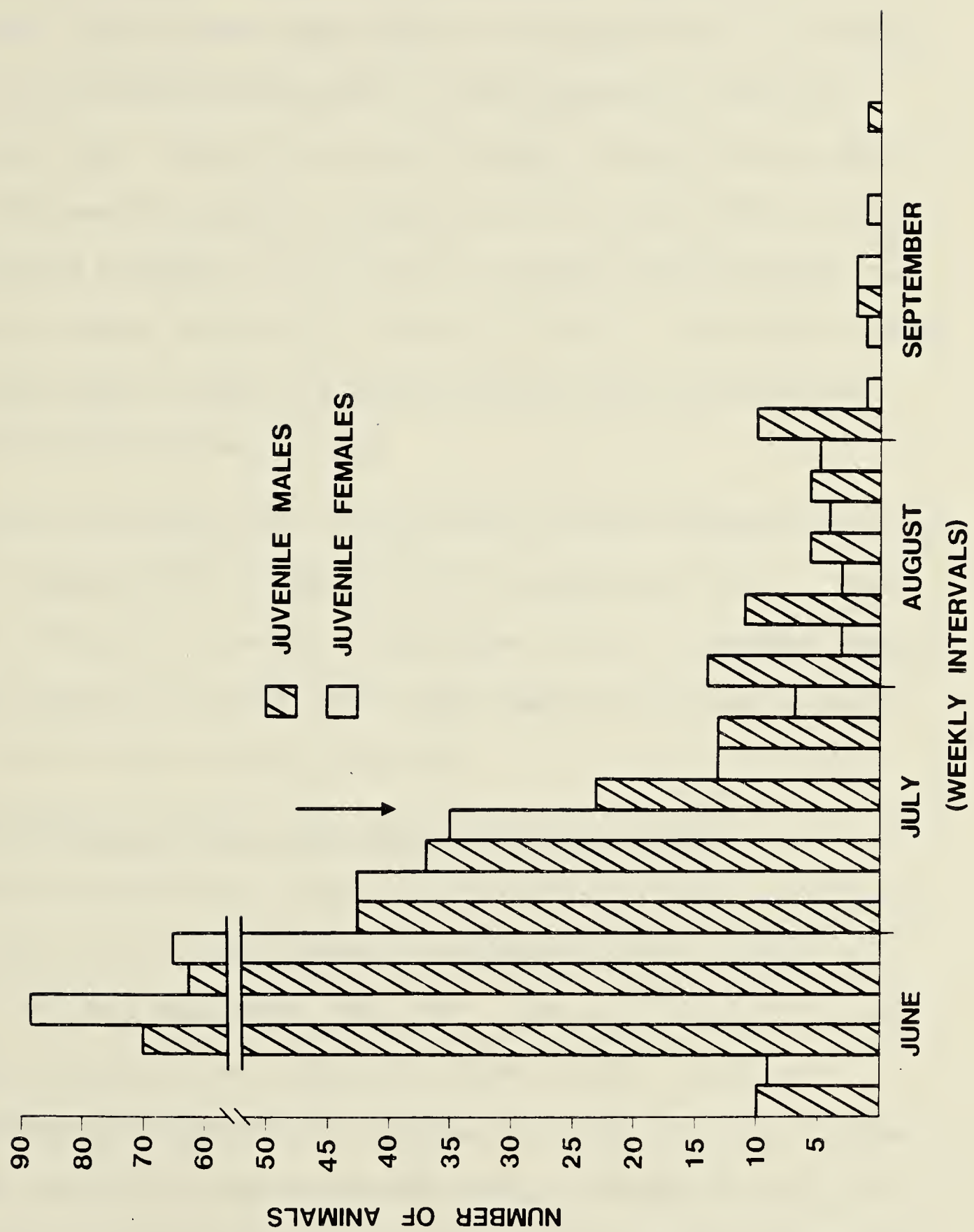




Figure 1: Date of first capture of juvenile arctic ground squirrels.

The week of first capture only for each individual is given. Most juveniles that emerged on the control area were captured and marked by the end of the fifth week after the first juveniles emerged (indicated by arrow). Animals captured after this time were likely immigrants.







and most juveniles born on the study area had been captured by mid-July, the time at which I first captured juvenile males known to have dispersed. Approximately equal numbers of untagged males and females were captured before mid-July (Fig. 1); more males were captured after this time. The ratio of males to females captured during the first five weeks of juvenile emergence in 1977 and 1978 (223:240) was significantly different to the ratio of juveniles captured during the rest of the season (86:40) ( $\chi^2_1 = 16.03$ ,  $P < 0.001$ ). Thus, more untagged males than females entered the population after most juveniles born on the study area had been tagged.

These data indicate that juvenile males usually dispersed, whereas juvenile females did not. Females did not disperse as adults; I show elsewhere (Chapter 3) that some adult males did so. In general, female kin that survived to become adults were likely to live near to each other; this was very unlikely for males.

#### Size and overlap of female home ranges through the season

Sizes of female home ranges ranged from (mean  $\pm$  s.e.) a maximum of  $2196 \pm 475.3 \text{ m}^2$  ( $N = 16$ ) in April to a minimum of  $1573 \pm 203.8 \text{ m}^2$  ( $N = 25$ ) in early June, 1978, and  $3153 \pm 460.4 \text{ m}^2$  ( $N = 21$ ) in April to  $1505 \pm 188.9 \text{ m}^2$  ( $N = 35$ ) in late June in 1979. These are measured from the meadows only, and thus constitute minimum estimates. Although trends are suggested by these data, no significant variation in the size of female home ranges during different parts of the season was found in either year ( $P > 0.1$ ; Kruskal Wallis test). Nor was there significant variation in the degree of overlap of female home ranges during different parts of the season ( $P > 0.1$ ; Kruskal Wallis).



Significant differences in the degree of overlap of home ranges of closely, distantly, and unrelated females were found in all two week periods after April during 1979 ( $P < 0.05$ ; Kruskal Wallis test) (Fig. 2). Values for distantly related females were intermediate to values for closely and unrelated females during May and June. Post hoc Mann Whitney U tests indicated that closely related females overlapped significantly more than unrelated females during the periods after April ( $P < 0.05$ ), and that the overlap of distantly related females was not significantly different to either of the other classes of female during any period ( $P > 0.1$ ).

Results from 1978, when distantly related and unrelated females could not be distinguished, were similar to the 1979 results. Significantly greater overlap of closely related females was found in July (Mann Whitney U test,  $P < 0.05$ ) in 1978, indicating that greater acceptance of close relatives continued after juveniles became independent.

In only one case (in 1978) did a female in an observation area live further than neighbouring distance (see Methods) from at least one of her close relatives. This female moved back toward her family group in 1979 (see animal #9, Fig. 3).

#### Interactions between adult females

A total of 1135 interactions between adult females were recorded during 696 hours of observation in 1978 and 1979. Of 412 interactions between closely related females, 126 (30.6%) were amicable, 194 (47.1%) were agonistic, and 92 (22.3%) were identification (Table 1). Of 723 interactions between females that were not closely related, 42 (5.8%)







Figure 2: Percent overlap of home ranges of closely, distantly, and unrelated female arctic ground squirrels during 1978 and 1979.

Bar gives mean + s.e.

Number of pairs of closely, distantly, or unrelated females used for calculating mean is indicated above each bar.

Star above group of bars indicates significant variation in overlap of home ranges ( $P < 0.05$ , Kruskal Wallis test).

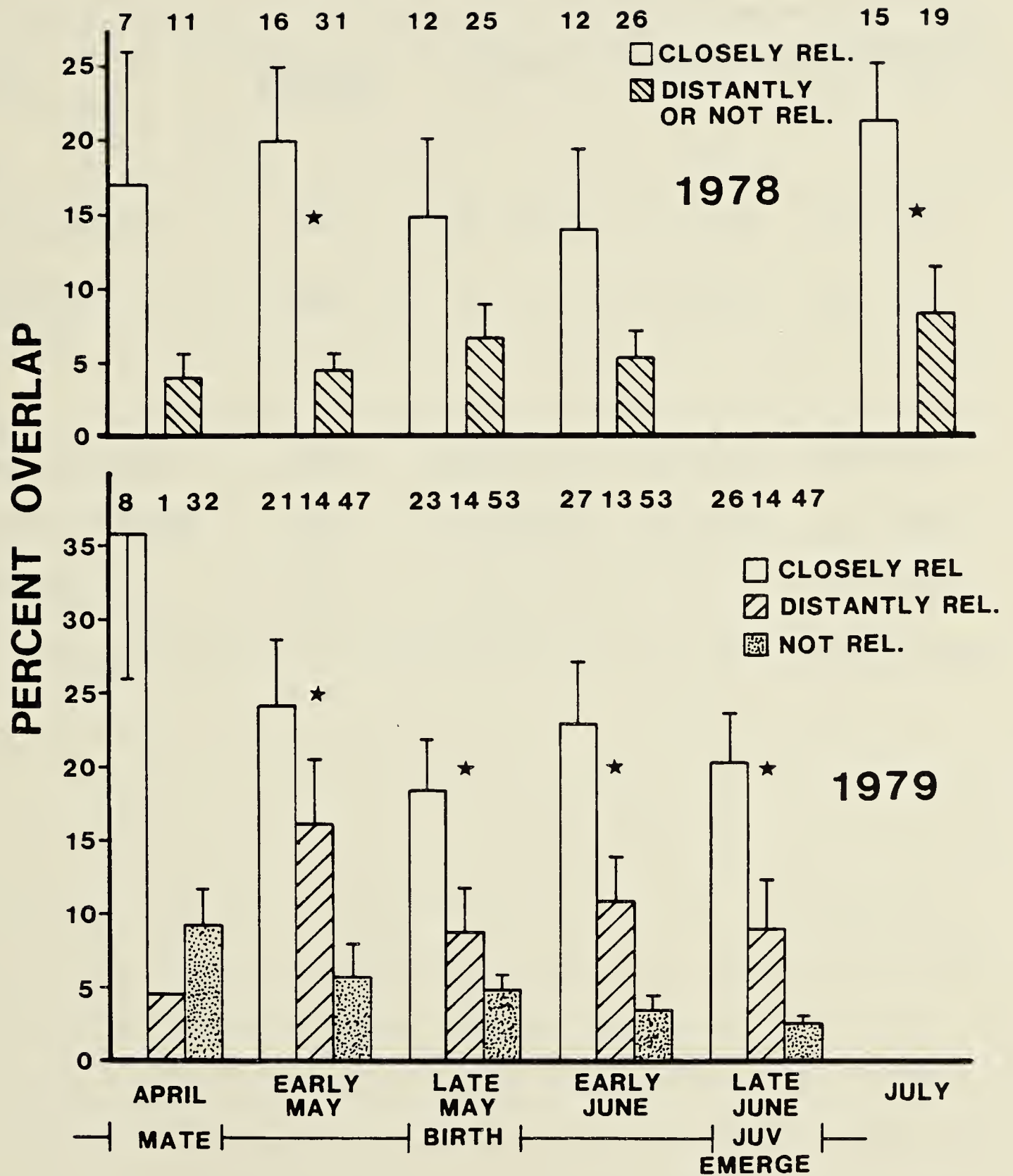




Table 1: Types of interactions observed between adult female arctic ground squirrels of each class of relationship during 1978 and 1979.

Females	Total int. observed	Amicable #	%	Agonistic #	%	Identification #	%
<u>1978</u>							
Closely related	142	26	18.3	73	51.4	43	30.3
Distantly or unrelated	297	8	2.7	264	88.9	25	8.4
<u>1979</u>							
Closely related	270	100	37.0	121	44.8	49	18.2
Distantly related	116	13	11.2	95	81.9	8	6.9
Unrelated	310	21	6.8	270	87.1	19	6.1





were amicable, 629 (87%) were agonistic, and 52 (7.2%) were identification. Thus most interactions between females were agonistic, but close relatives were more likely than other females to interact amicably.

To further investigate this aspect, I compared the proportions of (total amicable : total agonistic) for interactions recorded between the two (1978) or three (1979) classes of female (Table 1). Interactions were significantly more amicable and less agonistic between closely related females in both years (1978:  $\chi^2_1 = 43.11$ ; 1979:  $\chi^2_2 = 45.09$ ;  $P < 0.001$ ). Ratios were similar for distantly and unrelated females in 1979 ( $\chi^2_1 = 2.35$ ,  $P > 0.1$ ). Thus close relatives responded differently and more amicably to each other than did other classes of females.

I looked more directly at interactions that involved allogrooming. The 16 instances of allogrooming observed between adults were between closely related females (13), between females of unknown relationship (2), or between a mother and her yearling son (1). No instances were recorded of allogrooming between females known to be distantly related or unrelated, between males, or between adult females and unrelated males. Allogrooming between adults occurred most often in the early spring when at least one of the females had not mated, the time at which female home ranges overlapped most (Fig. 2). No allogrooming was observed during late May and early June when juveniles were underground. Five cases were observed during late June when juveniles were emerging and when some closely related females clumped their young (below).

#### Distribution of natal burrows and family movements

Natal burrows of arctic ground squirrels were usually small holes,



opened from underground (there was no loose earth to indicate the site of the hole), and located close to a major burrow system. These small holes were usually found by watching to see where females carried nest material (dried grass and other dead material), although digging activity on a major burrow system during early May was a good indication that a natal burrow would appear nearby.

After giving birth, the female always entered and emerged from the natal burrow when carrying nest material, or when disappearing for a long period, presumably to feed the young. Natal burrows were sometimes plugged at night with loose earth plugs, then re-opened in the morning (c.f. McLean, 1978, for S. columbianus). On a few occasions, females entered, but re-emerged from, a major burrow system nearby before going to the natal burrow. Females often delayed entry to the natal burrow if another squirrel was nearby, and never entered if the other squirrel was not a regular resident of the area. All indications were that females attempted to keep the location of natal burrows hidden from other squirrels. However, it was unlikely that resident males did not know the locations of natal burrows in their areas, as they were observed to put their heads down natal burrows, and occasionally entered them for a few seconds.

Positions of natal burrows were noted with reference to the grid system and distances between them measured from a map. Most females used more than one natal burrow during the period that the young were underground (Fig. 3), and up to four movements of young before emergence were recorded. Although some litters emerged at the natal burrow, most females moved their young on to a major burrow system at the time of





Figure 3: Distribution of natal burrows and movements of families of arctic ground squirrels on one observation area in 1979.

Ages of females:

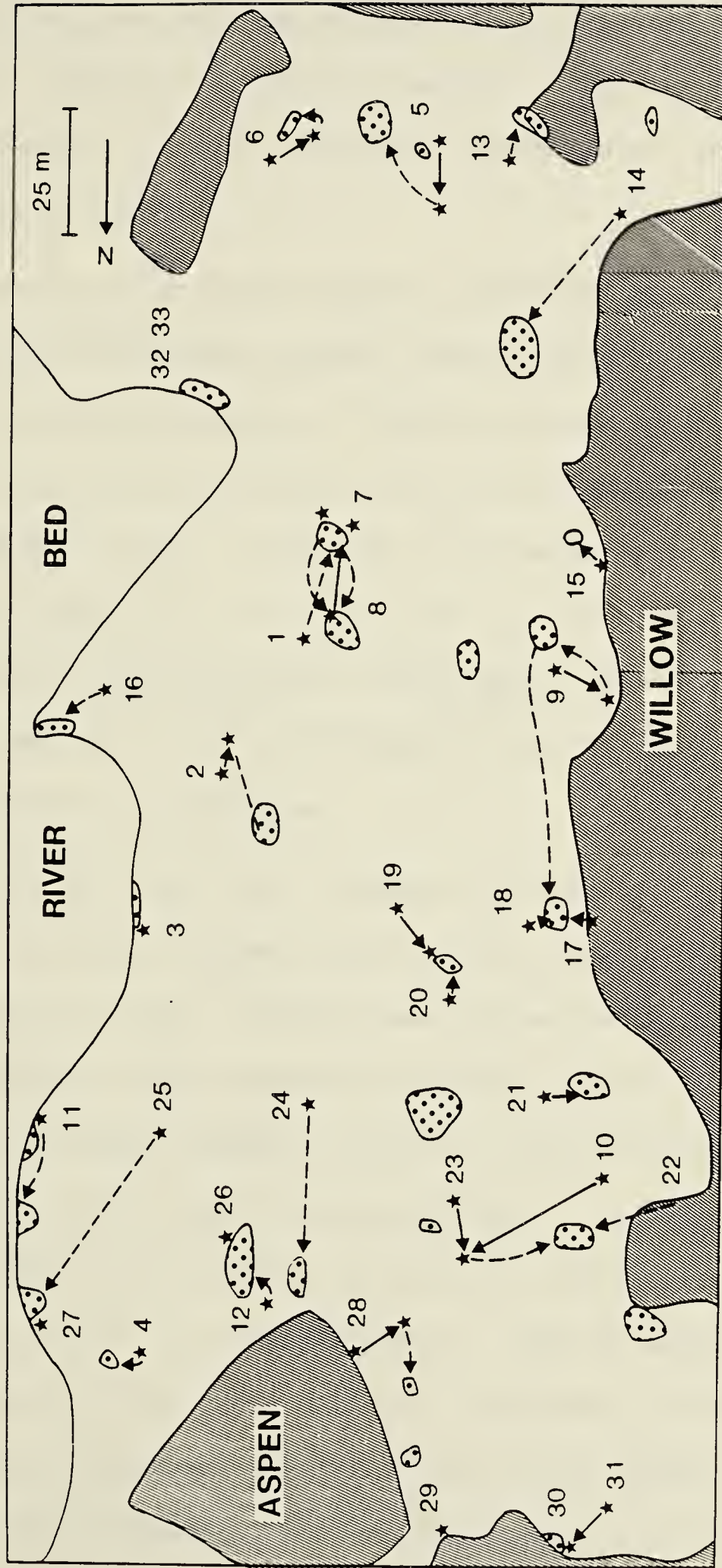
Numbers	1 - 5,	3+ years old.
	6 - 12,	2 years old.
	13 - 33,	1 year old.

Family groups were made up of the females numbered:

I: 1, 7, 8, 9, 15, 17, 18, 19, 20.  
II: 2, 16. (Some relationship was likely with #3.)  
III: 4, 11, 12, 24, 25, 26, 27.  
IV: 5, 13, 14.  
V: 10, 21, 22, 23.  
VI: 29, 30, 31.

Females 7, 23, 30, 32, 33 all lost young. Movements of pre-emerged young by 8 and 10 to the burrow system or natal burrow of 7 and 23 occurred after the litters were lost.





∴ MAJOR BURROW SYSTEMS

—▶ MOVEMENT BETWEEN NATAL BURROWS

★ NATAL BURROW

---▶ MOVEMENT OF YOUNG AT EMERGENCE



emergence, and some movement between burrow systems after emergence also occurred. Movements of young at emergence were not always to the nearest major burrow system; the largest recorded move was of 95 m past four burrow systems.

For the following analysis comparing distances between natal burrows of closely related, distantly related, and unrelated females, measurements were from the natal burrow in which the female gave birth, and were taken to the natal burrow being used by the nearest female of each class at the time of birth. Distances to the natal burrow of the nearest sister (mean  $\pm$  s.e.;  $28.0 \pm 2.84$  m,  $N = 12$ ) were not significantly different to the distances to the female's mother ( $27.8 \pm 3.36$  m,  $P > 0.1$ , Mann Whitney U test on 1979 data); thus the nearest of either of these was used in the analysis.

Females located their natal burrows significantly closer to the natal burrows of close relatives than to natal burrows of unrelated females in 1979 ( $P < 0.001$ , Wilcoxon test for matched pairs, Table 2). The mean distance to natal burrows of distantly related females (42.6 m) was similar to the mean distance of those of unrelated females (41.9 m), but the variance of the former was greater (Table 2), and differences between distances to natal burrows of close and distant relatives were not significant ( $0.1 > P > 0.05$ , Wilcoxon). Similar trends were found in 1978; distances to the natal burrow of the nearest close relative were smaller than distances to those of the nearest distant or non-relative, but the differences were not significant ( $0.1 > P > 0.05$ , Wilcoxon).





Table 2: Distance to nearest natal burrow of females of various classes of relationship during 1978 and 1979.

---

<u>1978</u> Distance (m) to nearest:		
	Close relative	Distant or non-relative
$\bar{X}$	34.9	44.3
s.e.	6.16	3.46
N	13	13

<u>1979</u> Distance (m) to nearest:			
	Close relative	Distant relative	Non-relative
$\bar{X}$	27.9	42.6	41.9
s.e.	2.37	4.66	2.63
N	34	22	36

There was no difference between distances to the nearest sister (28.0 m) and the mother (27.8 m) and the nearest of either of these was used.

Paired comparisons for which data were missing (e.g. where a female had no distant relative) were ignored in statistical testing (see text).





These data suggest that females located their natal burrows nearer to those of close relatives than to those of other females, with distances to distantly related females tending to be more variable. However, distances between natal burrows of closely related females were still relatively large (1978: 34.9 m; 1979: 27.9 m, Table 2). If closely related females tended to clump their natal burrows, I expected to find cases of two or more females with their burrows near to the same major burrow system. This occurred only twice, and one instance of two unrelated females with their natal burrows near the same major burrow system was also recorded. Also, greater overlap of home ranges of closely related females was found during this study (above), and these females would tend to have closer natal burrows as a consequence. I take these data to indicate that closely related females tended to locate their natal burrows closer together, but that there was no indication of related females grouping or clumping their pre-emergent young.

#### Movements of emerged young

In 1977 I noted several instances of two or three females moving their young to the same burrow system at about the time of juvenile emergence. During 1978 and 1979, ten instances of two females, and two instances of three females, clumping their young on one burrow system within one to three days of emergence were recorded. Seven were mother/daughter pairs, three were pairs of sisters, one was a group of three sisters, and one was a mother and her two adult daughters. All groups of sisters were yearlings, and the daughter of mother/daughter pairings was a yearling in all but one case. However, there were



few older animals of known relationship in the population in 1979 and these proportions are unlikely to reflect a strong bias towards clumping by yearlings. Numerous instances of clumping of juveniles by two or three females were noted in all three years in parts of the study area in which detailed observations were not made. No cases of clumping of juveniles by females known to be distantly related or unrelated were recorded.

In order to obtain an estimate of the proportion of females that clumped their young, I divided the total number of females that had at least one close relative living in the observation areas in 1978 and 1979 (51) into the total number that did clump (26). This indicates that 51% of the females that could have clumped their young with a close relative in 1978 and 1979 actually did so.

The combined factors of close relatives living near to each other, and the greater overlap of home ranges of close relatives, could result in higher probabilities of each female clumping with close relatives (CR) than with other classes of female (OF). Thus, although females were only observed to clump with close relatives, this may have occurred by chance. To test whether females clumped their young selectively with close relatives, or randomly with neighbouring females, I counted the neighbours that were CR and OF for each female that clumped her young, determined the mean overlap of the home range of this female with her neighbours in each of these two classes, and adjusted the ratio of CR:OF by the difference between the two mean overlaps. Overlap of home ranges, and those females that were neighbours, were determined from home range maps for the two weeks prior to the emergence of juveniles.



Only neighbours that brought up young were used in the analysis. Females other than close relatives were lumped since no clumping occurred with either distant or non-relatives. If overlap of home ranges was greater with OF than with CR, I did not adjust the ratio.

For example, if a female had three CR and five OF as neighbours during the two weeks before emergence of juveniles, and she overlapped by a mean of 25% with the three CR and 5% with the five OF, the ratio 3CR:5OF was adjusted to:

$$3 + \left( 3 \times \left( \frac{25 - 5}{100} \right) \right) : 5 = 3.6 : 5$$

Adjusted ratios were summed to give a total ratio of CR:OF for all females, that incorporated the difference in overlap of each female with her neighbours of differing relationship.

Data from 1978 and 1979 could not be considered independent since many individuals were present in both years, and too few cases in 1978 could be analysed adequately, so the following is for 1979 only. I could determine the home ranges of all relevant females for five pairs and one triplet. The unadjusted ratio of total CR:OF for these 13 females was 25:40, the adjusted totals were 29.68:40. This was significantly different to the observed ratio of 13:0 ( $\chi^2_1 = 14.46$ ;  $P < 0.001$ ) indicating that females clumped selectively with close relatives rather than randomly with neighbours.





## DISCUSSION

Individuals within a population must be shown to selectively favour relatives if the conclusion that nepotism occurs is to be drawn (Sherman, 1980a). In this study, I found i) that home ranges of closely related female arctic ground squirrels overlapped more than did home ranges of more distant relatives; ii) that close relatives interacted more amicably and less agonistically than did other females; and iii) that females selectively clumped their young with close relatives. These results suggest that closely related females shared resources to a greater extent than did more distant relatives. The differences in proportions of interactions suggest that mechanisms allowing females to identify close relatives were available. Selective favouring of relatives is indicated, and I conclude that female arctic ground squirrels exhibit nepotism.

Why did females clump their young?

Although females clumped their young at emergence, I found no indication that clumping of pre-emerged young occurred. Rather, distances between natal burrows of closely related females were relatively large, and only slightly smaller than distances between natal burrows of less closely related females. Even dispersion of nests has been shown to decrease the probability of nest predation in both colonial (Hunt and Hunt, 1975; Hutson, 1977) and territorial (Krebs, 1971; McLean, 1980) bird species. Well spaced natal burrows and movement of juveniles may be tactics for avoiding predation which, in the case of close relatives, are opposed by there being some small advantage to locating burrows closer together.



Families of young were easily located after emergence, thus any benefits derived from keeping them down cryptic natal burrows were probably lost. Possible benefits to individual females from clumping their young at emergence include:

- 1) More adults are watching for predators. Females spent more time in watching postures, and tended to vocalise more, during the period of juvenile emergence than during other periods in all three years of this study (Chapter 3). This may particularly have been a benefit when males intruded. Alarm calling at mammalian predators and at predatory birds tended to occur through large portions of the colony (c.f. Carl, 1971; Melchior, 1971; Sherman, 1977; Dunford, 1977b); thus females with litters on separate but adjacent burrow systems may have derived as much benefit from others watching for predators, as did females that clumped their young. But only those females directly subject to attacks vocalised at intruding males. Two or three females with clumped young would presumably be more likely to detect an intruding male than would one.
- 2) Defence of young. The only interspecific predators against which young could conceivably be defended were weasels (Mustela sp.), but none were ever seen in the area. Female ground squirrels were not successful in driving off males that attacked young, although they certainly attempted to do so, and may have caused enough distraction that some young were saved. Two or three females could presumably cause more distraction than one.
- 3) Presentation of a larger number of young. By "concealing" her



litter among those of other females, each female could increase the probability of survival of her own young. Clumped young may have been slightly easier to find than single litters, but I found little difference. Neither intruding males, nor intra-specific predators, killed all young when emerged litters were attacked (the most successful attacks recorded were a male ground squirrel that killed nine of ten juveniles in two litters, and a Goshawk Accipiter gentilis that took three of five young from one litter over several days). If only some young die, then a female would be less likely to lose some or all of her young if they were grouped with others.

These benefits are typical of those usually suggested for colonial species (McCracken and Bradbury, 1977; Hoogland and Sherman, 1976) and do not require that females be related for the benefits to be accrued. However, clumping with non-relatives could result in greater costs than clumping with relatives. For example, females that clump presumably act as lookouts for all juveniles on the burrow system, thus would suffer a cost in lost inclusive fitness if (distantly) related young that could have been protected died while non-relatives were protected; or, injuries could be sustained during the clumping process since non-relatives interacted more aggressively than did relatives (see Hoogland, 1979, for a more detailed analysis of the costs sustained by colonially living ground squirrels). My observation that only some females clumped their young, even when closely related females were available nearby, suggests that benefits are not always derived from this tactic. If relatives are available, and some benefit may be derived from clumping,







then females should clump preferentially with relatives.

#### The basis of nepotism among females

Females that exhibit nepotism must have some means of determining which individuals in the population are their relatives. Despite lack of dispersal by female arctic ground squirrels, immediate neighbours had only a moderate probability of being related (compare sample sizes in Figure 2; a neighbouring female was two to three times more likely to be a distant or non-relative as a close relative), and all females had individuals other than close relatives as neighbours. Thus indiscriminate sharing of resources or clumping of young with neighbours would not result in selective favouring of relatives; discrimination must be based on other factors. The results of Wu et. al. (1980), in which pigtail macaques (Macaca nemestrina) were found to recognise genetic relatives without benefit of prior familiarity, suggest the possibility of direct identification of genetic relatives. However, until alternative evidence is available, familiarity resulting from shared natal experiences is the most likely mechanism on which nepotism is based (Sherman, 1980a). Prior to their emergence, young ground squirrels are unlikely to interact with individuals other than their mother and siblings. Where mixing of litters before emergence has occurred in unusual circumstances (S. beldingi, Sherman, 1980a; S. richardsonii, G. Michener and L. Davis, Department of Zoology, University of Alberta, pers. comm.), introduced juveniles have been accepted. In S. beldingi, fostered individuals interacted with their foster family as with close relatives after emergence, and with their real family as with non-relatives. It seems likely that the behaviour



would be similar in arctic ground squirrels.

Sherman (1980a, p. 535) argues "... that nepotism among female Belding's ground squirrels is limited by historical infrequency of interactions with distant relatives in situations favouring cooperation". Sherman could identify no simple mechanism that would allow female Belding's ground squirrels to identify distant relatives. Such a mechanism may exist for arctic ground squirrels. During this study, all females that clumped young were close relatives. The young so clumped were therefore distant relatives. If this has been the pattern in evolutionary time, then arctic ground squirrels that favoured those individuals with which they interacted at the time of their emergence as juveniles would have a high probability of favouring distant relatives. My data are inconclusive, but suggestive, on this point. Values for overlap of home ranges of distant relatives were intermediate to values for close and non-relatives. Distances between natal burrows of distant relatives, and interactions between distant relatives, were more similar to those for non-relatives than to those for close relatives. If arctic ground squirrels favoured distant relatives more than non-relatives but less than close relatives, then they would be more similar to some primate species, which show decreasing cooperation as degree of relatedness decreases (Kurland, 1977), than are Belding's ground squirrels which do not distinguish between distant and non-relatives. This suggests the hypothesis that nepotism is limited more by the absence of mechanisms allowing identification of relatives than by the historical frequencies with which relatives have interacted. More data are needed comparing



the behaviour of adult arctic ground squirrels from litters that were clumped, with the behaviour of distant relatives from litters that were not clumped, before further evaluation is possible.





## CHAPTER 3

# PATERNAL BEHAVIOUR AND INFANTICIDE IN ARCTIC GROUND SQUIRRELS

## INTRODUCTION

Infanticide, defined here as the killing of conspecific young (Sherman, 1980b), has received increasing attention in recent studies of vertebrates (Hrdy, 1979; Chapman and Hausfater, 1979; Dickeman, 1979; Sherman, 1980a, b). Although probably occurring at low frequencies in many species, it may be a widespread phenomenon. For example, in the ground squirrels (Marmotinae), it has been recorded in natural situations in eight species of Spermophilus and one of Marmota (Snyder, 1976; Sherman, 1980b). Obviously, determination that it does not occur is more difficult than observation of its occurrence. However, of the species in which it is known, only in S. beldingi has its documentation been more than anecdotal (Sherman, 1976, 1980a, b). Cannibalism by Arctic ground squirrels (S. parryii) has been recorded in both the laboratory (Cade, 1951; Mussacchia, 1954) and the field (Steiner, 1972; Holmes, 1977), but none of these authors observed the killing. Holmes's observations of adult males killing each other in a late spring appear to be unrelated to the context of infanticide, and Steiner's work provided little information on the ecological context in which the infanticide occurred. I present here data i) on ten instances of infanticide by male arctic ground squirrels, in six of which the killing episode was observed, and ii) to support my interpretation that territorial behaviour by adult males serves to prevent infanticide. Hence males can be regarded as providing protection for the young.



Paternal behaviour in mammals is limited by physiological constraints (Pianka, 1978) and is generally restricted to group defense (e.g. Zebras, Equus quagga, Klingel, 1969) or provisioning (e.g. wolves, Canis lupus, Fox, 1971). Ground squirrel social systems are either polygynous or polygamous, and multiple paternity of litters may occur (Sherman, 1980b; Michener, in prep.). Thus even the animals themselves may have difficulty determining paternity, and one might predict that paternal behaviour was unlikely. Paternal care has been rejected for some species (Sherman, 1977, 1980a), but Barash (1975) argued that male alertness enhances the survival of juvenile Hoary Marmots (Marmota caligata), and the description of territorial behaviour in M. flaviventris by Armitage (1974) suggests similar interpretations. Adult male arctic ground squirrels have been described as territorial (Carl, 1971; Green, 1977) and I hypothesised that male territoriality functions to protect young during the stages when they are susceptible to killing.

For protection to be concluded, males must be shown to be territorial during the period that the juveniles are dependent and are susceptible to killing. For this protection to be termed parental care requires that those young be related to the protector. In this study I monitored the timing of territorial behaviour by adult males, the patterns of movements made by adult males, the activity budgets of males and females through the active season, and the occurrence of infanticide. To investigate the predictions that:

- i) adult males would not kill young they were likely to have fathered, and



ii) non-fathers would kill young,

I removed all males (presumed fathers) from two areas after all females had been mated. My prediction would be supported if higher levels of infanticide and lower reproductive success were found in these areas relative to control areas from which males had not been removed.

#### METHODS AND STUDY AREA

Arctic ground squirrels were studied at an elevation of 600 m on a 60 hectare area located ten kilometres west of Haines Junction, Yukon Territory (61°47'N; 137°40'W). The experimental (removal) areas were two meadows, ten (1978) and one (1979) kilometres south of this control area. All study areas consisted of meadows interspersed amongst areas of willows (primarily Salix glauca) with scattered stands of aspen (Populus tremuloides) and spruce (Picea mariana). The 1978 experimental area was part of a large meadow in the steep-sided Alsek River valley, but in all other respects appeared similar to the 1979 experimental area and the control area, which were in a more open location at the entrance to this valley. Densities of ground squirrels in the two experimental areas were within the range found in the control area. Seasonal events such as the birth period and the period of juvenile emergence were similar in all areas. The study area is described in more detail elsewhere (Chapter 1).





### Trapping program

Squirrels were trapped weekly at each study area with National or Tomahawk box traps using peanut butter as bait. Traps were placed on major burrow systems and small burrow systems that squirrels were known to frequent. Approximately 120 traps were set weekly in 1977 and 200 in 1978 and 1979. I attempted to set approximately 1.5 traps per ground squirrel known to be resident in the area so that extra traps were always available to capture dispersing animals. Observations were curtailed during the period of juvenile emergence (mid-June until early July) in 1977 and 1978 in order to capture juveniles as they emerged, and many more traps were set during that period. Traps were set soon after the emergence of ground squirrels in the morning, and were left open for one to three hours.

On first capture, ground squirrels were tagged in both ears with individually numbered fingerling fish tags and sex was determined. On this and subsequent captures weight, wounds, and reproductive condition were determined. Animals in areas used for detailed observations and in experimental areas were dyed with individual patterns using "Clairol" blue/black human hair dye, or "Jamar D" (Nyanza Co.).

Wounds over the entire body were counted and classified as: small, less than  $4 \text{ mm}^2$ ; medium, between 4 and approximately  $100 \text{ mm}^2$ ; or large, greater than  $100 \text{ mm}^2$ . Because larger wounds presumably indicated more severe or more frequent interactions (several wounds could combine to become one larger wound) I calculated a total wounding index for each animal at each capture by computing:

$$[(\text{total small} \times 1) + (\text{total medium} \times 2) + (\text{total large} \times 3)]$$



and obtained a mean for each week from these values. Wounds generally healed quickly (c.f. Rose and Hueston, 1978, who found in Microtus pennsylvanicus that "moderate puncture wounds are referable to the preceeding 7 to 10 days", p. 188). Only some large wounds were scored in more than one week and very few were scored in more than two.

#### Home range and time budgets

Two meadows 750 m apart in the control area were gridded in 15 m squares with flags or stakes to allow accurate location of animals. The position, and activity at the position, of animals living in these areas were sampled instantaneously (Altmann, 1974) by scanning with binoculars (Bushnell 10 x 50 mm) and sampling each animal as it was encountered. Observations were conducted from stands 2.5 m high. A spotting scope (Bushnell 20x) was used to facilitate individual recognition of animals. The sampling interval varied from five to thirty minutes between years and observation areas, but remained constant within one year for each observation area. Observations were conducted during all parts of the day although most were made during the four hours immediately after ground squirrels emerged in the morning when activity was greatest. Observations were conducted on most evenings during the mating period.

Home ranges were drawn by plotting a minimum polygon (Hayne, 1949) from the above sightings. A minimum of nine sightings were required for a range to be drawn. Criteria used for drawing lines between points, for rejecting outlying points as "excursions", and for calculating overlap, have been described elsewhere (Chapter 2). Any part of a home range for which there was no overlap with the home range of any other individual of



the same sex was termed exclusive.

My primary purpose in calculating a time budget was to compare the proportions of time spent in each behaviour by each sex during each part of the season. Sampled behaviours were condensed into seven categories (Table 1). Time budgets were calculated by dividing the number of times an individual was observed in a particular behaviour by the total number of times that individual was seen during each two week interval, converting this to a percent, and obtaining a mean percent frequency for each behaviour by totalling for all individuals and dividing by the number of individuals observed. A minimum of seven sightings during a two week interval was required for an individual to be included in the calculation of the time budget for that interval. Behaviours such as vocalising or tail flicking, which occurred while the animal was engaged in one of the seven major categories, were sampled separately as "subsidiary" categories. Time budgets for subsidiary categories were calculated separately. For example the proportion of time spent vocalising was obtained by subtracting from the "alert" total (or other categories in which vocalising also occurred) the number of times the animal vocalised while in "alert" (or other behaviours) and calculating vocalising as a separate major category, as described above.

### Interactions

The instantaneous sampling program was interrupted to allow detailed descriptions of interactions to be noted as they occurred. The "scan" described above was continued from the point at which it stopped when the interaction was first noticed.







Table 1: Categories of behaviour used in the field and for development of a time budget.

<u>Categories used in field sampling</u>	<u>Categories used for time budget</u>
Feed, head up Feed, head down Moving while feeding	Feeding
Lying/basking Sitting, four feet on ground Grooming	Resting/maintenance
Sitting, forefeet off ground Alert, body erect	Alert
Walking Running	Moving
Aggressive interactions Amicable interactions Identification interactions Sexual interactions	Interactions
Digging Gathering nest material Carrying nest material	Burrow associated behaviour
Investigate holes Sniffing ground	Investigate
<u>Subsidiary categories used in field sampling</u>	<u>Associated behaviour</u>
Tail flick	Any
Vocalisation	Any
+Scent marking, scratch at burrow	Investigate

---

+ See Kivett, et al. (1976) for an analysis of scent related behaviour in this species.



Interactions were divided into agonistic, amicable, "identification", and sexual. In summary (see Chapter 2; Carl, 1971; and Watton and Keenleyside, 1973, for more detailed descriptions), agonistic interactions involved chases, fights, and parallel runs (see below); amicable interactions involved greeting (kissing), body sniffing, and allogrooming; and identification interactions included situations where one animal approached another but the result could not be unambiguously assigned to one of the other three categories. Sexual interactions occurred when a male approached an estrus or pre-estrus female and either attempted to sniff her anal region or chased her if she ran off. Males sometimes jumped back several times from females that remained stationary, but approached again rapidly or sniffed the spot where she had been sitting, if she ran off. Interactions with post-estrus females that involved sexual components were assigned as identification.

A parallel run occurred when two animals ran side by side, one to two metres apart, for one or more metres. Both animals arched their backs, arched and flared their tails, and attempted to remain alongside the other during the run. A parallel run ended when the two animals veered towards each other, bumped together, then bounced apart. These interactions very rarely involved fights; more often the animals sat several metres apart vocalising before initiating another parallel run, often in the opposite direction to the previous run. Interactions involving parallel runs lasted for up to 45 minutes; parallel runs of up to 40 metres in length were recorded.

Interaction rates were calculated weekly. Values for number of



interactions per individual per ten hours were calculated from the formula:

$$\left( \frac{\sum \left( \frac{\text{number of interactions observed during each hour}}{\text{number of individuals present during that hour}} \right)}{\left( \frac{\text{total number of hours observed}}{\text{during week}} \right)} \right) \times 10$$

i.e., a rate was calculated for each hour using the number of individuals observed in the meadows during that hour (obtained from sampling program). These values were summed for all hours within the week and the summation was divided by the total number of hours observed. This method compensates for variation in the number of animals that may be available to interact, for example at different times of day. It does not allow for variations in the probabilities of particular individuals interacting (for example, neighbouring individuals are more likely to interact than are individuals at opposite ends of the observation area). Michener (in press) has discussed variation in interaction rates obtained by different methods of calculation in more detail.

#### Dispersing and excursioning by adult males

Dispersal and excursioning by adult males were determined as follows:

- 1) An animal was considered to have dispersed if he was trapped more than 100 m from the area he usually occupied, and never returned.
- 2) If the above occurred, but he was subsequently re-trapped two or more times in his usual area, he was considered to have been on an excursion.
- 3) A male's "usual" area was defined as any area in which he was trapped at least twice during any consecutive four week interval. Males that





were re-trapped two or more times in a usual area after an absence of three or more weeks were considered to have been on an excursion. For example, if 1 = trapped and 0 = not trapped, and each number represents one week of trapping, a sequence such as 11001000101 resulted in the animal being considered as "on excursion" during the period of three zeros. Adult males were generally captured more consistently than suggested by this example, some animals being captured during every week of the season.

- 4) To produce Figure 6 (p. 82), the week after the last week of capture in the usual area was used as the week in which the dispersal or excursion occurred. The only exceptions were cases in which the first capture outside the usual area was during the same week as the last capture within. Data from all three years were used. Since an animal's usual area in the early spring could only be determined from captures during the previous fall, the first two bars for April and early May include data from 1978 and 1979 only; bars after this period include data from 1977 and 1978 only.

#### Experimental removal of adult males

All adult males resident in experimental areas were removed by live-trapping between 18 May and 21 May in 1978 and 1979. Females were giving birth at this time. These males were released up to 30 km away and none returned to the experimental areas. All had been resident for at least ten days prior to the removal. In 1978, additional males were removed on 28 May, 9 June, and 17 and 18 July. A total of nine males were removed in each year. It was assumed that males that were removed had fathered most of the young born in the experimental areas.



## RESULTS

A total of 785 ground squirrels were captured 5625 times during the periods 28 April through 15 October, 1977; 16 April through 26 September, 1978; and 7 April through 8 July, 1979. More than 1300 hours of observation were conducted from 5 May through 4 August, 1977; 20 April through 11 August, 1978; and 12 April through 4 July, 1979. Of these, approximately 100 (1978) and 50 (1979) hours were conducted in the experimental areas between 15 May, when females began to give birth, and 30 June, when all juveniles had emerged. Approximately similar numbers of hours of observation were conducted on the control area during each week through the season, with the exception that few observations were made during the period of juvenile emergence in 1977 and 1978, whereas trapping was curtailed during this period in 1979 to allow increased observation.

### Wounding and interaction rates

Interactions between arctic ground squirrels often resulted in one or both of the antagonists being wounded. For the following analysis, I assumed that all wounds were acquired during intra-specific interactions.

Wounding of adult males followed consistent patterns during all years (Fig. 1). Two peaks in wounding occurred, the first during the mating period and the second in early to mid-July when juvenile males were beginning to disperse. Most wounds had healed by late May, and wounding levels were low during June. By early August, wounding had dropped to moderate levels and fluctuated for the rest of the season.

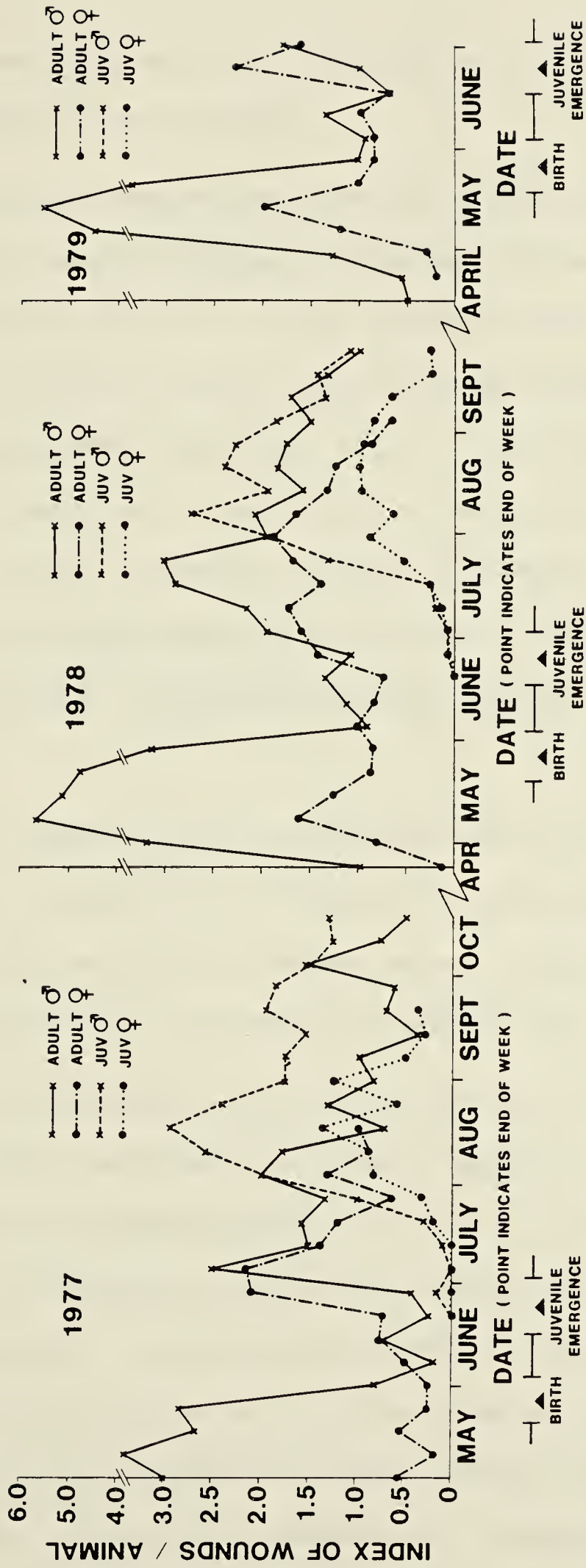




Figure 1: Index of wounding of arctic ground squirrels during the active seasons of 1977, 1978, and 1979.

To obtain the wounding index, the wounds on an animal when captured were counted and classified by size. Calculation of the index is described in the text.







A third small peak occurred in the late fall in 1977 (trapping stopped before the equivalent time in 1978).

Wounding of adult females and juveniles is presented for comparison (Fig. 1). A small peak in wounding of females occurred in the spring, after which wounding remained at low or moderate levels until juveniles began emerging in mid June, when a large increase occurred. Wounding continued at higher levels until late July and August, when females began entering hibernation. Juveniles were rarely wounded until four to six weeks old when an increase occurred, particularly for males. Wounding of juvenile males remained at moderate to high levels through the rest of the season. Wounding of juvenile females remained at lower levels.

Data for the types of interactions observed and the rates at which they occurred are presented for 1978 and 1979. Although I am concerned here primarily with interactions between males, I present data on interactions between males and females for comparison.

Except for interactions initiated by males with females, interactions between arctic ground squirrels were usually agonistic (Fig. 2). Highest rates of interactions between males were during the mating period. Highest rates of interactions initiated by females with males were between mating and parturition. Interaction rates during the periods when juveniles were underground and emerging were generally low. The number of hours watched were lower after late June and peaks suggested by the data may be partly an artifact of sample size. However, these peaks do correspond to peaks recorded for wounding (Fig. 1).





Figure 2: Rates of interactions between males, and between male and female arctic ground squirrels during 1978 and 1979.

Sample sizes: H = number of hours observed during week.  
I = number of interactions observed.

Time line (in weeks) begins in mid April at the time that females were beginning to emerge from hibernation.

Note change in horizontal scale.







With the exception of sexual interactions initiated by males with females, non-agonistic interactions generally occurred at low rates. Few non-agonistic interactions occurred between males; none was amicable.

#### Overlap of home ranges and parallel runs

In Figure 3 I present an example showing the interactions involving one central male (CM) during the mating period and during the four weeks prior to the emergence of juveniles. CM's home range and those of his neighbours are outlined. Five points emerge from this example:

- 1) There were large areas of overlap of home ranges of males during the mating period, but little overlap in the later period.
- 2) CM's home range decreased in size after the mating period (thus some females mated by CM early in the season may have been resident outside his subsequent home range).
- 3) CM won and lost interactions both within and outside his "home range" during the mating period and those interactions were distributed through most parts of the home range. During the later period interactions generally occurred only near boundaries.
- 4) Parallel runs were relatively more common after the mating period.
- 5) Parallel runs corresponded to boundaries of home ranges.

All five points were similar for all males that remained resident through these periods. My purpose in analysing these data was to investigate whether or not males could be considered territorial during the period that juveniles were underground. I used data from all males in 1978 and 1979 for points 1) and 4) in order to investigate this aspect.

The degree of exclusiveness of male home ranges increased from





Figure 3: Home range and interactions of a central male during two periods in 1979.

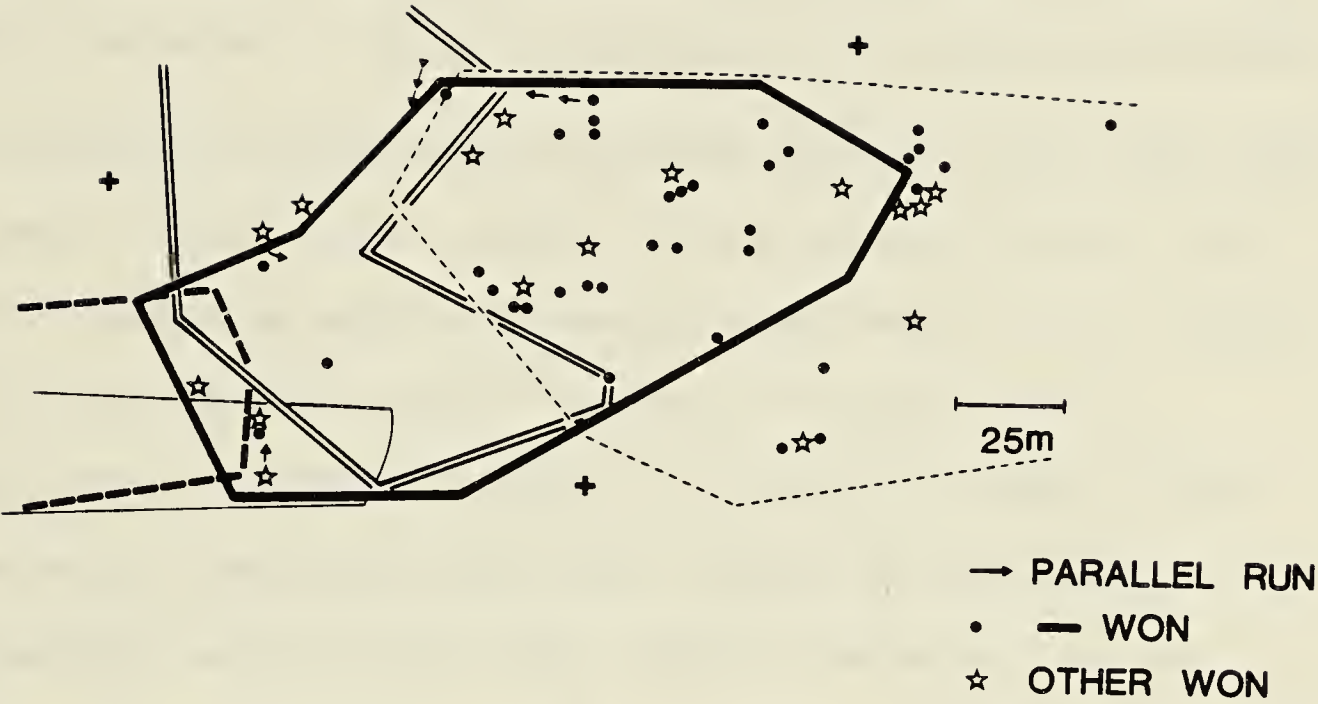
Home ranges of central male outlined in solid black.  
Other ranges are those of his male neighbours.

Similar outlines of home ranges indicate the same male during each period.

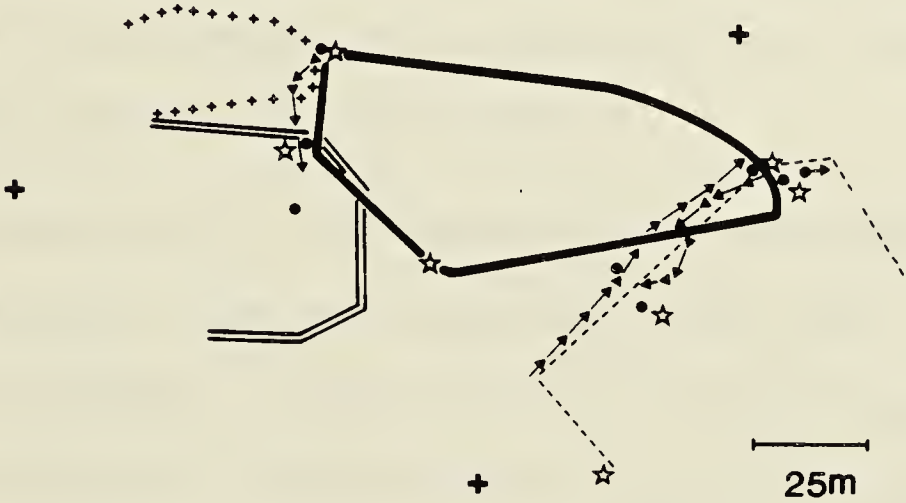
The point at which an interaction began is indicated by dots and stars. Interactions always involved chases so that it was possible to determine a winner. Where the animals reversed the chase so that the "chasee" became the "chaser", a new point is indicated.



MATING PERIOD



JUVENILES UNDERGROUND





approximately 28% during the mating period to 75-80% by the time females were giving birth in both 1978 and 1979 (Fig. 4). There was little overlap of home ranges of males during the period that juveniles were underground and emerging, and some indication of an increase in overlap (exclusiveness decreased) in July when juveniles were becoming independent.

Males attacked and chased other males that came into their home ranges during all parts of the season. However, during the mating period, when home ranges of males overlapped considerably, other males were not always attacked if a male was with a female that was in or near estrus, but they were attacked if they attempted to approach the female. Males that knew an estrus female was in the area, but who had lost contact with her, sometimes passed by each other within a few metres without interacting while apparently searching for the female. It was not possible to determine whether interactions observed during the mating period were related to estrus females, or to space (and hence males were attempting to establish territories), or to both.

After the mating period intruding males were invariably attacked; strange (non-neighbour) males were sometimes chased right through the home ranges of neighbours so that the chase ended well beyond the home range of the chasing male. As the season progressed the proportion of interactions between males that involved parallel runs increased, with significantly more interactions involving parallel runs during the period when juveniles were underground than during the mating period (Table 2). Neither animal was obviously dominant, or the "winner", either during or after interactions that involved parallel runs. Rather, each moved back





Figure 4: Change in exclusiveness of male home ranges through the active season during 1978 and 1979.

Bar gives mean + s.e.

Number of home ranges included in calculation of the mean is indicated above the bar.



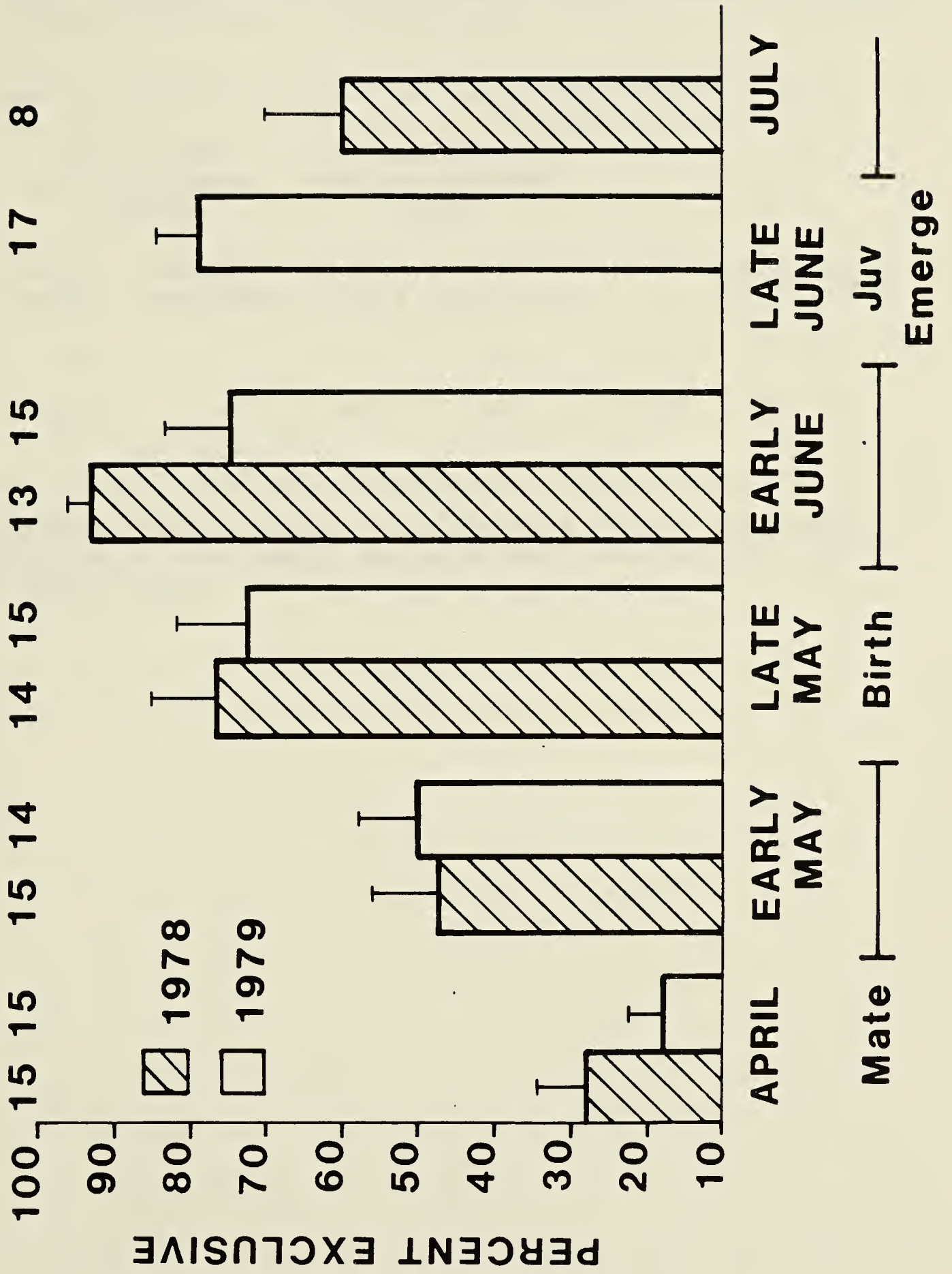




Table 2: Percentage of interactions between adult male arctic ground squirrels involving parallel runs during the mating period (15 - 30 April) and the period when juveniles were underground (14 May - 11 June) in 1978 and 1979.

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Year	Total number of interactions observed		% of interactions involving parallel runs		$\chi^2_1$	Significance*
	Mating period	Juveniles underground	Mating period	Juveniles underground		
1978	88	71	11.4	39.4	16.93	P < 0.01
1979	174	98	14.4	29.6	9.05	P < 0.01

---

\* A significantly higher percent of interactions between adult males involved parallel runs during the period when juveniles were underground in both years.



into his area and away from the common boundary. Parallel runs were never observed between two males that were not neighbours. Because they occurred on or near the boundaries of home ranges, parallel runs were more obviously related to space than were any other interactions between male arctic ground squirrels. I take these data to indicate that interactions between males became more strongly related to space and to boundaries as the season progressed, and that males defended territories from the time that females were giving birth.

#### Time budgets of male and female arctic ground squirrels

Males and females behaved differently. Densities of animals (and hence sample sizes) were highest in 1979, and I present the time budget from that year in detail (Fig. 5). The following description is consistent with the time budgets recorded in all three years (Table 3).

Females fed and engaged in nest and burrow related activities more than males, whereas males were usually more alert and investigated their areas more than did females. Males moved around more than females before mid June, particularly during early May (c.f. Table 3). Males lay around on burrow systems "resting" more than females during the periods when juveniles were underground and emerging. Males spent more than 50% of their time during the period when young were underground in resting and alert behaviours during all three years of the study. Males vocalized significantly more than females when juveniles were underground in 1979, whereas during and after the emergence of juveniles and early in the season females vocalized more than males (although see Table 3). The greater vocalizing by females in July, 1979, was close to significantly









Figure 5: Time budget of male and female arctic ground squirrels in 1979.

Bar gives mean + s.e.

Number of males or females included in calculation of each mean is indicated above "Feed" graph.

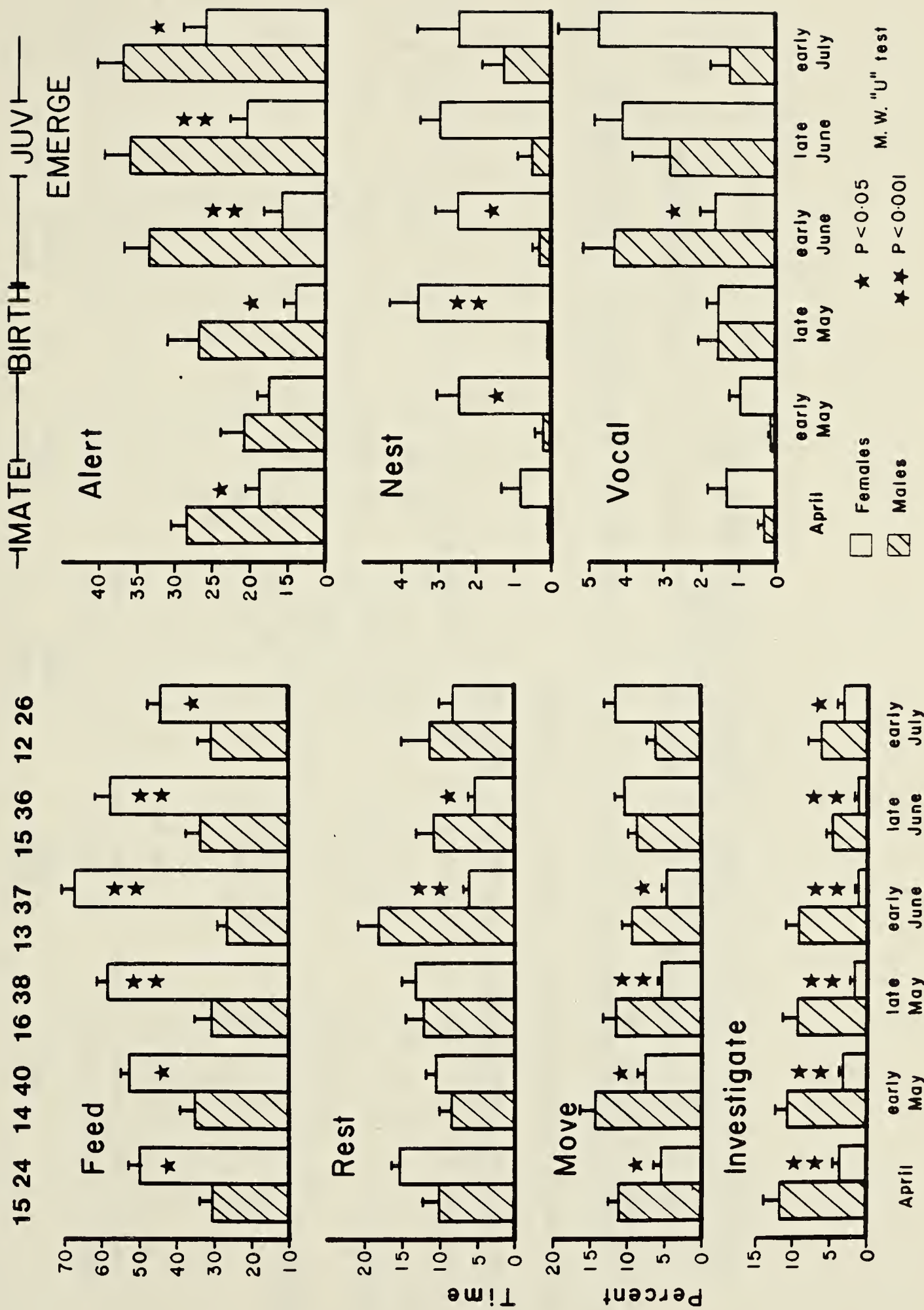




Table 3: Differences in time budgets of male and female arctic ground squirrels during 1977, 1978, and 1979 (compare with Figure 5).

	April		Early May		Late May		Early June		Late June		July	
Year	77	78 79	77	78 79	77	78 79	77	78 79	77	78 79	77	78 79
♂ Feed	--	F* F*	F	F* F*	F	F* F*	0	F* F*	F	-- F*	M	0 F*
♂ Rest	--	0 0	0	0 0	0	0 0	0	M* M*	M	-- M*	F	0 0
♂ Move	--	0 M*	M* M* M*	M* M*	0	0 M*	0	0 M*	M	-- 0	M	0 F*
♂ Investigate	--	M* M*	M* M* M*	M* M* M*	M*	M* M*	0	M* M*	0	-- M*	M	M* M*
♂ Alert	--	M* M*	0	M* 0	0	M* M*	0	M* M*	0	-- M*	F	0 M*
+ Nest & burrow	--	0 0	F* F* F*	F* F*	0	F* F*	F	F* F*	0	-- F	F	0 F
+ Vocalise	--	0 F	0	0 0	0	0 0	F	0 M*	F	-- F	F	F F

♂ Behaviours that usually fell in the 10 - 50% range.

+ Behaviours that usually fell in the 1 - 5% range.

Where means differed by greater than 5% (♂) or 1% (+) the sex (F = female, M = male) with the higher mean percentage is noted:

- \* indicates that the difference was statistically significant ( $P < 0.05$ , Mann Whitney U test).
- 0 indicates differences less than 5% or 1% (as above).
- indicates no data or too few data gathered to allow comparison.





higher ( $P = 0.08$ ).

In no instance was a behaviour significantly different in one direction (e.g. males more than females) during one period, and significantly different in the opposite direction for the equivalent period in a different year (Table 3). The only period during which there was considerable variation in whether males or females spent more time in particular behaviours was July, when young were becoming independent. Thus males and females apportioned their time in reasonably similar ways in all years.

#### Dispersal and excursioning by adult males

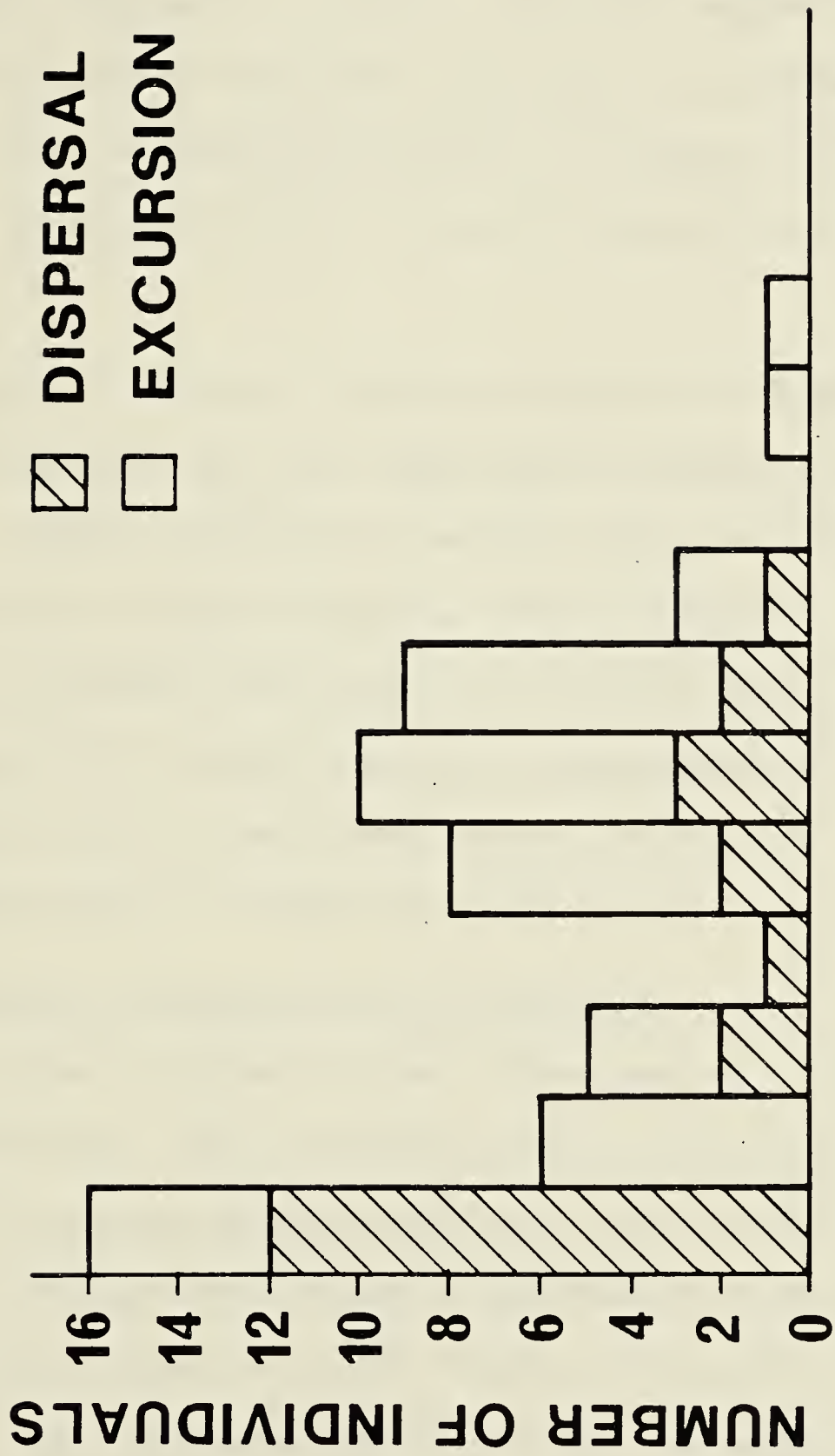
Arctic ground squirrels followed the usual pattern found in the genus Spermophilus of juvenile males dispersing, juvenile females remaining near their natal areas (Chapter 2). However, some adult males also dispersed and some were trapped on excursions (Fig. 6). A total of 101 males were trapped the minimum number of times required (see Methods) to be included in this analysis. Of these, 60 dispersed, were captured on an excursion, or disappeared for an extended period. Of these 60, the natal areas of 28 were not known and four dispersed from their natal areas as yearlings (yearling male arctic ground squirrels are usually capable of breeding and are therefore regarded as adults). In order to obtain some estimate of the number of adult males that left the areas to which they had previously dispersed as juveniles, I subtracted these 32 (28 + 4) animals from the total of 101 to give 69 males known to have established residence outside their natal areas. I subtracted the same 32 animals from the 60 known to have left their area of residence as adults, either





Figure 6:    Dispersal and excursioning by adult male arctic ground squirrels during 1977, 1978, and 1979.

First two bars include data from 1978 and 1979. All other bars include data from 1977 and 1978.



May | June | July | Aug | Sept | Oct  
 ( BI-WEEKLY INTERVALS )

Birth Juvenile Emergence





permanently or on an excursion (Fig. 6), giving 28 of 69 adult males (40.6%) who left their area of residence for some period after having previously dispersed as juveniles. This is a minimum estimate since the data do not include any animals which may have dispersed and disappeared, or which made an excursion but were not trapped on that excursion. These animals are included in the 41 (i.e. 101 minus 60) not included in Figure 6.

These data indicate that adult males did not disperse once and then become sedentary; many males made further movements. The two peaks in Figure 6 further indicate that movements were most likely during the mating period and during late June and early July (when juveniles were emerging and before they dispersed), and were unlikely at other times. Equal numbers of animals dispersed or made excursions during April and May; excursions were more likely during June and July. Half the animals that dispersed did so during the mating period.

#### Infanticide: its perpetrators and occurrence

Ten cases of infanticide were either seen or inferred during this study (Table 4). Three cases of killing of young before emergence occurred; only one individual survived. For 20 parous females that were captured within five kilometres of the study area and that subsequently gave birth in captivity in 1979 the mean litter size was  $6.4 \pm \text{s.d } 1.46$ , range 4 - 11. Excluding the litter of 11 (the largest litter seen in the field at emergence was of eight young, see Table 5), mean litter size was  $6.1 \pm 0.99$ , range 4 - 8,  $N = 19$ . Assuming an average litter size of 6.1 at birth, approximately 17 of 18 young died in the above



Table 4: Evidence for the ten instances of infanticide recorded and the history of the male perpetrators.

Juvenile stage	Number of cases	Evidence	Male history	Response of female(s)
Before emergence	3	Killing episode observed.	2 became resident after mating period.	2 remained in area, nipples regressed.
			1 became resident after female was mated.	1 successfully brought up one remaining juvenile.
After emergence	3	Killing episode observed.	3 became resident after the female was mated.	7 moved remaining young outside the area usurped by the male.
				2 lost all young, remained in area.
	4	Dead young found, new male in area, females wounded.	2 moved into new area on day of killing.	
			1 became resident after the female was mated.	
			1 resident non-breeder, emerged late from hibernation.	



three attacks. Three cases of killing of emerged young were observed and four were inferred (evidence in Table 4). In the three cases seen, 16 of 21 young in four litters were killed. All killing was by adult males. In nine of the ten cases the killer was very unlikely to have fathered the young, either because he was not resident in the area when the female mated (8 cases), or because he was a non-breeding male that emerged late from hibernation (one case). The tenth case was an individual that killed a litter outside the area in which he was normally resident, but the distance moved (approximately 100 m) was not far enough to rule out his having fathered that litter.

When juveniles were emerging, some females, including three that had lost young, made excursions outside their usual areas and investigated the litters of neighbouring females. In 23 instances in which females were observed to approach close enough to sniff juveniles on burrow systems that were outside the females' usual home ranges, no attacks were recorded. I found no indication that females committed infanticide.

Pre-emerged young were killed by males that had become resident in the area after the mating period. On the three occasions observed, the male remained down the natal burrow for 70 and 150 seconds, and 36 minutes. In the first of these, the mother brought several dead young to the surface and they were consumed by her and by neighbouring females. In this and another case, the female had previously been entering the natal burrow frequently, presumably to feed the young. After the killing, she stopped entering this or any other natal burrow, and her nipples regressed within three days. Both females had lost all young. In the third case, one juvenile emerged





from the natal burrow the day after the killing, but this female had brought up seven young in both 1977 and 1978. It seemed unlikely that she would produce only one in 1979.

Emerged young were killed by males that:

- 1) moved in from some other area on the day of the killing (2 cases);
- 2) extended their range on the day of the killing (4 cases) having become resident nearby after the mating period;
- 3) killed in an experimental area (1 case, see below)..

Of the three cases observed, one involved a male which extended his range to include the burrow system on which a female and her adult daughter had their litters. This male was attacked constantly by the two females over a period of four hours, during which he actively searched for the emerged young of the older female, and killed four. The daughter's young had not emerged and she successfully moved six to a burrow system 15 m away, on two occasions being attacked by the male while carrying a juvenile. The females interspersed their attacks on the male with almost continuous calling. The emerged young that survived did so by hiding, either under bushes or down nearby burrow systems. The male left these females and their remaining young alone after this occasion, although they remained on the burrow system nearby, and he often sat and watched them from the burrow system that he had usurped.

In the second case a neighbouring male that had become resident nearby after the female was mated ran across to the burrow system on which her young had emerged four days previously, and went underground for ten minutes (the weather was cool and overcast and most of the young were



underground). The adult daughter of this female detected the male, ran about in an agitated fashion, and chased one of the two juveniles that were above ground away from the burrow system. The mother came back but could not enter the burrow; she attempted to dig and it appeared that the male had plugged the hole from underground. When the male eventually emerged she chased him 100 m, then returned. One dead juvenile was found at the burrow where all the digging had taken place. This female lost three of five young.

In the third case, I arrived in the study area while the male, who had extended his range to include the burrow systems occupied by two females and their litters, was killing a juvenile. My disturbance allowed one of these females to move her last juvenile (of 4) to a neighbouring burrow system on which her two adult daughters had their litters. The other female lost all six young. The male remained resident in the area.

Of the four cases of infanticide that were inferred I can provide some extra details to those given in Table 4 for three. One occurred in 1977 just outside the observation area. For approximately 2.5 hours I heard an unusual amount of calling coming from this site. On investigation I found a dyed male from the observation area on a burrow system on which I had ear-tagged nine of twelve young of two litters the previous day. Two of these lay dead on the burrow system, the two adult females were heavily wounded whereas two days previously they had been unwounded, and the male remained resident in that area until the spring of 1979, when he disappeared.



In a second case, a yearling male whose testes remained abdominal emerged late from hibernation onto his natal area. His mother and two sisters brought up young in the area. In late June he began extending his range and on 30 June killed some of the litter of his mother's sister (an aunt) living nearby. As on other occasions, all females moved their young out of the area usurped by the male. However this male was unusual for several reasons: i) He was one of only three males that remained on or near their natal area until the time of juvenile emergence in the yearling year (natal areas were known for 235 marked males). ii) He was subordinate to, and accepted by, the resident male and their ranges overlapped almost completely. Theirs was the highest proportion of overlap recorded during this study for any two males after the time females gave birth. The resident male was likely to have been his father. iii) Before extending his range he often interacted amicably with his sister's young, and on one occasion successfully chased off a neighbouring male that approached them. He continued to interact amicably with his sister's young after the killing.

A third instance, in 1978, involved a male that moved into a vacant neighbouring territory and killed all of one of the two litters in the area. He also attacked a juvenile from the second litter very aggressively several days later, but the pup escaped. One dead juvenile was found. The male remained resident in the area until the next spring, when he disappeared. Before moving he had interacted amicably with the litter of the central female in his previous territory. Ten days after he moved, she and some of her litter were also spending part of their time in his new area. This was the only instance recorded where a female appeared to







follow a male in his movements; however, the distances were relatively small and involved an extension rather than a change of range by the female.

Infanticide: did the males eat their victims?

I observed adult male arctic ground squirrels chewing on one mouse (Microtus sp.), the remains of two Snowshoe hares (Lepus americanus) and two dead juvenile arctic ground squirrels. In all cases the remains were abandoned after a few minutes with large portions of the carcass left unconsumed. Males sometimes returned to the carcass for a short time, but I suspect, as did Steiner (1972), that scavengers such as foxes and magpies usually eat young killed by ground squirrels. Given these indications that carcasses are not eaten rapidly, it seems unlikely that a male spending 70 or 150 seconds down a natal burrow could have consumed the young killed, nor were they carried off. One male that killed four emerged young carried two of them back to his original area but took only one below ground. The other two were left where killed. During this study I also found five other young dead from unknown causes lying on burrow systems. These were killed by bites to the head, neck, and upper body, as were the young seen killed, but were otherwise whole. These data, though sparse, suggest that males did not kill young in order to obtain protein and that they killed more than they could carry off or consume.

Infanticide: experimental removal of adult males

Two cases of killing of young before emergence and one case of killing after emergence described above occurred in the two experimental



areas from which all adult males were removed in mid-May. Males that moved in after the removal were assumed not to have fathered any of the litters emerging on the area. I tested two predictions:

- 1) That more females on the experimental areas would lose their litters than in the control area from which males were not removed.
- 2) That litter sizes in the experimental areas would be lower than on the control areas. This prediction follows from the observation that not all young always died when a male attacked a litter before emergence.

In 1978, two of 26 females on the control area and five of 15 on the experimental area did not bring up young (Table 5). This difference was not significant ( $0.1 > P > 0.05$ , Fishers exact test), although the predicted trend of greater loss on the experimental area did occur. The mean litter size at emergence of 6.1 on the control area was significantly higher than that of 4.5 recorded on the experimental area ( $P < 0.01$ , Mann Whitney U test), supporting prediction 2.

Replication of this experiment in 1979 produced results that were not significant for either prediction (Table 5). I therefore looked more directly at those females that lost litters on the control area during the two years. Due to natural loss of males, five of these eight females had natal burrows sited in the territories of males that established residence after the mating period. These males were unlikely to have fathered those young, and in effect, those females were equivalent to females on the experimental area. By looking at male territories rather than at "experimental" and "control" areas I found that only three of 58



Table 5: Reproductive success of female arctic ground squirrels in control and experimental areas during 1978 and 1979.

---

1978: Number of females bringing up young.

	Successful	Unsuccessful
Control	24	2
Experimental	10	5

$0.1 > P > 0.05$  Fishers exact test

1978: Number of juveniles per litter at emergence.

	Mean*	S.d.	N	Range
Control	6.1	1.00	14	4-8
Experimental	4.5	1.43	10	2-6

$P < 0.01$  Mann Whitney U test

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1979: Number of females bringing up young.

	Successful	Unsuccessful
Control	32	6
Experimental	13	3

$P > 0.1$  Fishers exact test

1979: Number of juveniles per litter at emergence.

	Mean	S.d.	N	Range
Control	5.3	1.34	19	1-7
Experimental	4.9	1.27	9	3-7

$P > 0.1$  Mann Whitney U test

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\* Females that brought up no young are not included in calculation of the mean.





females (5.2%) lost litters that were located in territories of males with whom they were likely to have mated, whereas 13 of 37 females (35.1%) lost litters that were located in territories of males with whom they were unlikely to have mated (data from both years were combined). This difference was significant ( $\chi^2_1 = 14.5$   $P < 0.01$ ), indicating that females were more likely to lose their litters if they were located in the territories of males that established residence after the female was mated, and who therefore were unlikely to have fathered those young.

#### DISCUSSION

These data show i) that adult male arctic ground squirrels defend territories during some parts of the active season; ii) that adult male arctic ground squirrels commit infanticide; iii) that if the male who was resident in an area during the mating period defends that area as a territory while the juveniles are underground and are emerging, females in that area will have higher reproductive success; iv) that some males leave their areas while juveniles are emerging; and v) that males and females behaved differently, with males undergoing behaviours associated with vigilance (alert, lying) more than females during the period that the juveniles were underground. These results suggest that, by defending territories, males protect young in those territories. If he has fathered at least some of those young, then he can be regarded as giving parental care.



Four questions arise from these results. 1) Why are males territorial? 2) If males protect young, why do some males abandon their territories, even for short periods, at a time when young are emerging and are in need of protection? 3) Do males give misdirected parental care (male home ranges decreased in size after the mating period and some males dispersed, hence they may have fathered some young outside their territories and not fathered some of those within)? 4) Why do males commit infanticide? Although I cannot provide definitive answers to these questions, I will attempt, in the following discussion, to assess the validity of the various answers that may be proposed.

#### Why do males defend territories?

Juveniles derived protection, but this may not be the primary function of territorial behaviour by adult males. The following, although not exhaustive, is a list of likely hypotheses which may explain territorial behaviour by ground squirrels:

- 1) Defence of females to ensure access for mating (S. beecheyi, Owings, et. al., 1977; S. columbianus, Murie and Harris, 1978; Betts, 1973).
- 2) Defence of a limiting resource. Although food is probably the ultimate limiting resource for any species (Lack, 1954), it has not been shown to be limiting for any species of ground squirrel (although see Yeaton, 1972), and has been considered unlikely as the primary resource defended by S. columbianus males (Murie and Harris, 1978) and S. beldingi females (Sherman, 1980b). Other resources that may be defended include a home site (including



protection from predators), a hibernaculum (Carl, 1971), or seeds and seed stores (Appendix 1).

- 3) A cause of dispersal of juveniles (Marmota flaviventris, Armitage, 1974; S. parryii, Green, 1977), possibly in order to reduce inbreeding (Yeaton, 1972; Sherman, 1980b).
- 4) To reduce the transmission of ectoparasites or disease (Hoogland, 1979) or reduce the likelihood of discovery or capture by inter-specific predators (Sherman, 1980b).
- 5) To reduce infanticide. This was considered likely for Marmota caligata by Barash (1975) although he did not describe this as a consequence of territoriality. Sherman (1980a,b) argues that female S. beldingi protect young both directly and through territorial behaviour.
- 6) Decrease the probability of misdirected parental care (Sherman, 1980b).
- 7) Provide access to a supply of juveniles.

I am concerned here specifically with territorial behaviour by males during late May and June, the period when juveniles are underground and are emerging, and are susceptible to predation. If males are territorial during this period in order to obtain access to females for breeding (hypothesis 1), they should continue to defend those territories until the end of the season and should emerge and mate on those territories in the spring. My data suggest that exclusiveness of male home ranges decreased in July. Also, some males dispersed in June and July and others dispersed in the spring. Carl (1971), although describing male arctic ground squirrels as territorial throughout the active





season, considered that the system of territorial defense changed through the season with animals defending hibernacula in the fall. These observations indicate that some breakdown in the territorial system occurs during the later parts of the season and in the next spring. Some animals may gain access to females in the spring as a result of territorial behaviour the previous May and June, but I consider this unlikely to be the only hypothesis explaining territorial behaviour and vigilance during the post-mating period.

Some benefit is presumably gained through defense of potentially limiting resources other than females, such as home sites or food (hypothesis 2). There were unused burrow systems in the study area during all years of this study suggesting that home sites were not limiting. Vegetation is most lush in this area during late May and June (Douglas, pers. comm; pers. obs.) and it appeared unlikely that food would be limiting during this period. However, males might defend territories in order to obtain food during other parts of the season. Males collected seeds for storage during July and August, probably for use during hibernation (Appendix 1). The seed crop failed in 1978, thus was not always reliable, and could be limiting in some years. I cannot reject the hypothesis that food or seed stores were obtained as a result of territorial behaviour in May and June; but I also cannot reject the hypothesis that territories were necessary for obtaining these resources.

Juveniles began to disperse in mid-July in this area and continued to do so until the end of the season (Chapter 2). Wounding of juveniles increased in July, but I cannot discriminate between the alternative



hypotheses that these were obtained either on the natal area, or after leaving. Green (1977) suggested that juvenile male arctic ground squirrels dispersed as a result of increased aggression by adults. But increased aggression towards juveniles may bear no relation to territorial defense. Green provided no data on this point. I consider that dispersal of juveniles in July and later is unlikely to be related to territorial defense by adult males in May and June, particularly since some adult males left their territories before mid-July.

In order to reduce the transmission of ectoparasites or disease, or to decrease the likelihood of discovery or capture by predators (hypothesis 4), territorial behaviour should be directed at both sexes. Females were not excluded from male territories and the home ranges of individual females overlapped with those of up to three males. Interactions initiated by males with females were often either sexual or identification rather than agonistic. These are unlikely to be functions of male territoriality during May and June.

Female reproductive success was higher in areas in which males remained resident from the mating period until after the juveniles had emerged. This suggests that infanticide was reduced if a male that bred in an area also defended a territory in that area during May and June (hypothesis 5). I consider the questions of whether males provided misdirected parental care (hypothesis 6) or obtained access to juveniles to kill (hypothesis 7) below. Both of these may have occurred. Females could not prevent incoming males from killing; thus if killing was prevalent, selection should act on males to protect the young of females with whom they mated. Advantages in fitness would accrue if



males fathered at least some of the young in their territories, and I suggest that protection of young is a major function of territoriality by adult males during May and June.

#### Absence of males from their territories

Why did some males abandon their territories, even for short periods, at a time when the young were emerging and were susceptible to killing? Males may leave either because it has become uneconomical to defend the resource(s) previously defended (Gill and Wolf, 1975), or because there is some advantage to moving which outweighs any cost(s) sustained. By moving through unfamiliar areas, males may sustain greater predation than by remaining in a known area (Murray, 1967), and may lose young in the former area. Thus it is likely that there is some cost to moving. Most movements by males after mid-June were excursions. Few males dispersed, suggesting that males were investigating the surrounding area. Possible benefits to be derived from moving to a new area include:

- 1) A territory of superior "quality" could be obtained.
- 2) Males could avoid inbreeding in their original area (since females breed as yearlings). Sherman (1980a) found that male S. beldingi that were most likely to move after breeding were those that had achieved the most copulations.
- 3) Grass seed began maturing in early July, and juvenile males began dispersing in increasing numbers from mid-July. Thus males that moved before this time would avoid competition with dispersing juveniles, and would both arrive in the new area before seeds there had been harvested and leave before establishing seed stores







in the previous area.

These benefits would only be derived by males that moved to a new area. A further benefit would be derived by males that either dispersed or made excursions:

- 4) Males would gain access to juveniles that they were unlikely to have fathered.

I have argued that food is unlikely to be limiting in June, suggesting that it may no longer be worth defending. However, it seems unlikely that males with abundant food should go looking for it elsewhere if by doing so they suffer some costs. It is also unlikely that, by leaving, a male would significantly decrease competition for food among the many juveniles emerging on his area (Michener, in prep.). Males might move in search of better seed crops. In 1977 many males collected seeds and seeds were abundant; 18 of 18 males that were captured, dispersed or made excursions after mid-June. In 1978 few males collected seeds and the seed crop failed; 14 of 36 males that were captured dispersed or made excursions after mid-June. This does not indicate that greater movements were made when the seed crop was poorer.

These arguments do not suggest that males searched for areas of better quality. However, although most males returned, some did disperse, and I cannot reject the hypothesis that males were searching for better territories, but that these were not usually found. Assuming that benefits such as those I have described could be derived from dispersal, then males attempting to disperse would be subject to two



opposing pressures. A new area might be found, but if the previous territory is taken over by another male, or if young in the previous area are killed during the former male's absence, he may lose either territory or fitness. The length of absences from the former territory should depend on factors such as: how many young were fathered there, what the probability of another male establishing residence is, and whether the territory was of good or poor quality. I suggest that some or all of the benefits I have listed could be accrued, and that males made excursions during late June and early July in order to search for new areas in which to establish residence.

Males that made movements during late June and early July would encounter juveniles that they were unlikely to have fathered whether or not they established residence elsewhere. However, I found no indication of "raiding" males (Steiner, 1972) during this study (i.e. males entering an area for a short time, committing infanticide, then leaving). All cases of infanticide on emerged young were by males that had moved to the area after the mating period; in five cases they moved in on the day of the killing. On seven occasions in which marked males were observed in areas outside their territory on an excursion, no juveniles were attacked. On two of these occasions the male ran off when approached by a juvenile. It appeared that infanticide was a consequence when males attempted to establish residence in a new area.

#### Why did males commit infanticide?

The following is adapted from lists of possible reasons for infanticide prepared by Hrdy (1979) and Sherman (1980b). Both argue



for the adaptiveness of infanticide in that at least some individual(s) benefit. Sherman divides infanticide into two major categories; those in which parents benefit, for example if the mother is stressed by the demands of an offspring and would be better able to rear another at a later time; and those in which parents lose. As noted by Sherman, these may be impossible to distinguish in practice, particularly where males perpetrate the killing. Hrdy includes "pathological" killing, where no individuals appear to derive benefit, as a separate class of infanticide. Such cases have been reported for arctic ground squirrels in the laboratory (Cade, 1951; Musacchia, 1954; pers. obs.) although as noted by Hrdy:

"some animals [may have been] selected to respond to danger and potential threats...by eliminating the current offspring (like the pursued kangaroo who jettisons her joey) and deferring further parental investment until a more opportune birth." (Hrdy, 1979, p. 20)

Thus explanations in terms of individual advantage may always be erected, even where the behaviour appears to be an unnatural response to an unnatural environment.

Possible gains accruing to male arctic ground squirrels that commit infanticide include:

- 1) Food. The juvenile may be eaten. As noted by Steiner (1972), male arctic ground squirrels left carcasses lying on burrow systems during this study. It was doubtful that much food benefit was derived.
- 2) Females. By removing dependent young, the male may cause females to come into estrus more rapidly. This is likely for







Langurs (Presbytus entellus; Hrdy, 1979), and the "Bruce effect", in which females spontaneously abort or resorb young, may be an extreme example (see Schwagmeyer, 1979; Labov, 1980). Some female ground squirrels may recycle into estrus if unmated immediately after emergence in the spring (S. beldingi, Morton and Sherman, 1978; S. richardsonii, Michener, pers. comm.), but female arctic ground squirrels do not breed again in the same season after losing young. Females that lose young may overwinter and breed more successfully in subsequent seasons (Michener, 1978). Not enough females lost young during this study for me to assess directly the likelihood of this argument. However, young are weaned once they come above ground and the primary role of females after this time is as lookouts. Thus males that kill post-emergent young do not remove the physiological drain of lactation from females, although females without young may spend less time watching and more time feeding in preparation for hibernation. It seems likely that if the primary benefit derived by males was females that were better breeders in subsequent seasons, then killing would occur immediately after birth. My data from the control area, in which one case of killing of all but one of a litter the day before their emergence, and three cases of killing of post-emergent young, were observed, do not support this prediction. However, infanticide was suspected in some other cases in which females lost young before emergence, particularly where males established residence in an area that was vacated by the previous male. Also, infanticide on young



before emergence is more difficult to detect than on young that have emerged. More data are needed on these aspects.

- 3) Spite. Through killing unrelated young, a male could decrease the fitness of others, even if he endures some cost (Davis and Dunn, 1976; Pierotti, 1980). At present, data are not available to evaluate this possibility. In arctic ground squirrels it will require determination of whether males that kill have fathered young elsewhere.
- 4) Removal of competitors, either of the male, or of his offspring. Juvenile male arctic ground squirrels disperse (Chapter 2). Thus by removing young males from the population, a male could decrease the competition for territories and females experienced by his sons elsewhere. Young females are potential mates for the next season, yet were also killed. By killing all juveniles, a male presumably decreases the competition for food and other resources in the area. Also, females whose young were killed moved themselves and any young that survived out of the immediate area in which the male established residence, but they did not move so far that they would not have been accessible for mating the next spring. It is possible that some benefit was derived from removing other ground squirrels from the immediate area.

Males that could derive the most benefit from committing infanticide should be those that fathered juvenile males in the surrounding area, and those who avoid inbreeding by establishing residence away from their emerging daughters. Some further benefit in decreased competition in the new area of residence could also be accrued. Costs



suffered by these males include the possibility of wounds inflicted, either by mothers defending their young or by the original resident returning, and the possibility that young that were fathered in the area that was abandoned would be killed. I cannot resolve the paradox in this argument that those males that would derive the greatest benefit and should therefore leave, are also those that would suffer the greatest cost, and should therefore remain. I suggest that no simple explanation can be proposed for why some males commit infanticide. It does seem unlikely that all males would adopt the tactic of killing other males' young. Successful males on good territories could be selected to remain on those territories despite the possibility of inbreeding. Unsuccessful males on poor territories should be selected to move. However, although they are likely to gain by becoming resident in a new area, they would derive little benefit from infanticide and may suffer some cost. I consider it likely that not all males that moved would commit infanticide, and that some males would neither move nor commit infanticide. Thus, as found during this study, infanticide should occur at low frequencies, and may not occur at all in some years. Further work in this area will involve investigation of:

- 1) The number of years in which males breed. My preliminary data (unpubl.) suggest that males suffer a higher mortality than females and breed in a small number of seasons. Also, some males may delay breeding for one or more years (S. beldingi, Sherman, 1976; S. columbianus, Murie and Harris, 1978). For some of the factors I have discussed (e.g. inbreeding) to be relevant, males







should have a reasonable probability of breeding in more than one year.

- 2) Whether only some males commit infanticide, or whether it only occurs in particular circumstances.
- 3) Correlations between male movements and territory quality.
- 4) Whether infanticide may be "pathological" in that no animal benefits. If infanticide formerly provided some benefit which does not now accrue, the behaviour could be retained in the population for some time if little or no cost was incurred.
- 5) The occurrence of infanticide in other populations. Lack of observation of infanticide by Carl (1971) and Green (1977) suggests that it may only occur in some populations. However, these authors may not have made enough detailed observations at the proper times for the behaviour to be observed. It was only during the third summer of this study that infanticide was observed on the control area.

#### Behaviour of females

The observations reported here provide some insight into the behaviours that female arctic ground squirrels might exhibit in mating. Once infanticide is established in a population, females should act to minimise the probability of losing young. I argue elsewhere (Chapter 2) that females combine their litters at emergence so that young are better protected. Several females could share lookout duties and act together when attempting to fight off infanticidal males. However, neighbouring males can continually monitor events in nearby areas, and, as was observed once during this study, could presumably



enter and kill at opportune times. Males should only commit infanticide in neighbouring areas if they could not have fathered those young. By mating with, or consorting with, more than one male in the spring, females could confuse the issue of paternity, thus ensuring that neighbouring males would not attack their young. This leads to two predictions:

i) Males should chase intruders well beyond their territory boundaries.

This was observed during this study. ii) Where a male disappears,

infanticide should only occur if a new male establishes residence in

the area. Infanticide should not occur if the area is taken over by

neighbours. Multiple mating by females has been established in

S. beldingi (Sherman, 1980b), but in this species only females and

yearling males regularly commit infanticide, and mothers can protect

their young against them. Male S. beldingi are wide ranging in

the spring, thus would have a low probability of fathering any particu-

lar female's young. Hence little selection for protection of young

by males could occur. Female S. columbianus may mate with more than

one male (Murie and Harris, 1978), but as with S. parryii, copulations

occur underground (Murie and McLean, 1980) and the extent of multiple

mating is unknown. Further work in this area will involve determining

whether males "remember" if they mated in the spring, and with whom;

whether females mate with more than one male; and whether multiple

paternity of litters occurs.

#### CONCLUSION

This discussion leads to the conclusion that male arctic ground



squirrels give some misdirected parental care. Since the home ranges of males change during the spring, they are unlikely to have mated all those, and only those, females resident in their subsequent territories. Males that protect young through territorial behaviour almost certainly protect some young that are not their own.

I have established that adult male arctic ground squirrels commit infanticide, although at low frequencies. Instances of infanticide greatly affected the reproductive success of the individuals involved, thus selection should act to minimise its occurrence. I argue that males maximise reproductive success by protecting young born in their territories, but that some move as a result of the combined possibilities of inbreeding if they remain where they are, and obtaining better territories elsewhere. Infanticide appears to be a consequence of such movements; males on excursions did not kill young ground squirrels. I suggest that one way females minimise the probability of infanticide is by mating or consorting with several males, thus confusing paternity. Infanticide has been suggested as a strong selective force in other species of ground squirrels (Dunford, 1977a,b; McLean, 1978; Sherman, 1980b). The interpretations offered here may provide insights into the behaviour of other species in which infanticide is as yet poorly documented.





## SUMMARY AND CONCLUSIONS

Arctic ground squirrels in the southwest Yukon live in colonies in which males defend territories, and females tend to associate selectively with kin. As reported by Carl (1971), the extent to which males defended territories varied through the season, with my data indicating that spatial exclusiveness (c.f. Emlen, 1957) was most pronounced during the periods that females were giving birth and juveniles were underground. During the mating period, I could not distinguish between the alternative but not exclusive hypotheses that males defended females or space. Similar confusion may occur in the spring in Columbian ground squirrel populations (S. columbianus):

"During the breeding season, a dominant male with a female in estrus within his core area sometimes faced an increased frequency of intrusions by neighbouring males.....In such cases the resident male was dominant in the majority of interactions but intruders were more persistent than at other times of the year." (Murie and Harris, 1978, p. 2407.)

This description could apply equally well to arctic ground squirrels.

The social system of Richardson's ground squirrels (S. richardsonii; the other species to which arctic ground squirrels may be closely related, Liapunova and Vorontsov, 1970) appears to be in marked contrast:

"I believe that the reduction in the size of male ranges [during the pregnancy-lactation phase] was in part due to the aggressiveness of females which, in 1975, confined the males to an area where no females had their natal burrows. Confinement to this area would also account for the extensive overlap of male ranges." (Michener, 1979, p.135.)

The social system of male S. parryii appears to be more similar to that



of S. columbianus than to that of S. richardsonii. However, differences do occur. For example, male S. columbianus are probably longer lived and more sedentary than are male arctic ground squirrels, so that the probability of there being high frequencies of interactions between males in the spring due to their not having been neighbours in the previous year (c.f. Murie and Harris, 1978), may be higher in S. parryii. Hence arctic ground squirrels may appear to be either more territorial, or more aggressive, than Columbian ground squirrels.

The social system of female arctic ground squirrels may be more similar to that of female S. richardsonii than of female S. columbianus, since Michener (1979) reports some grouping of female kin in S. richardsonii. As yet, there are no published accounts of grouping of female kin in S. columbianus. Since some association of female kin appears to be the usual situation in the ground squirrels (Armitage, in prep.; Michener, in prep.), Columbian ground squirrels may be unusual in this regard. Differences between these species presumably relate, in part, to the different ages at first reproduction of females (S. parryii and S. richardsonii at one year, S. columbianus at two years). However, infanticide in arctic ground squirrels may cause selection for stronger associations between females in this species than in either of the others.

Male arctic ground squirrels protected young born on their territories from attacks by other male ground squirrels. I suggest that they behave paternally as a result, since there is some probability that they fathered young born on the territory. Resources such as a home site and food are presumably obtained along with the territory,





and territorial males could have a higher probability of surviving than males that did not defend territories (c.f. Carl, 1971). These benefits can be weighed against any costs sustained through protecting unrelated young. In S. beldingi, infanticide is perpetrated by adult females and yearling males. Females can defend their young successfully against these, but killing occurs at relatively high frequencies (accounting for a greater mortality of young squirrels than any other factor, Sherman, 1980b), and males could presumably be selected to protect young that they had fathered if those young could be identified. Sherman (1980a) describes the mating system in this species as "male dominance polygyny" (p. 511). Males cover large distances in search of estrus females and multiple paternity may occur; thus there is little chance that males could identify their own young. It seems likely that male arctic ground squirrels also cannot distinguish their own young from those emerging on the territory, since animals that committed infanticide moved to new areas before doing so. I suggest that female arctic ground squirrels should attempt to confuse paternity, but this should not occur to the extent that males are unlikely to have fathered any of the young born in their subsequent territories. Hence, males should show some spatial association in the spring, as was observed during this study, and females should mate only with the males in their immediate area.

Many differences were found between male and female arctic ground squirrels during this study. The active season of females was shorter than that of males. The foods taken by males and females were very similar, but some differences occurred in the timing of dietary changes,





probably in relation to the earlier entry into hibernation by females. Males and females behaved differently, presumably in relation to their different reproductive commitments. Males searched for estrus females during the mating period, then became territorial and watchful after mating was over; females spent most time feeding. Males dispersed, whereas females did not; thus females were more likely than males to associate with kin. Females exhibited nepotism by sharing space with neighbouring kin, by interacting more amicably with kin, and by clumping their young with kin. Males and females adopted different tactics during the hibernation period. These differences resulted in a social system in which males and females overlapped in space, but behaved relatively independently. I suggest that infanticide by adult males is a major factor influencing the behaviour of both male and female arctic ground squirrels. However, only some of the differences outlined above may be interpreted in the light of attempts by individuals to prevent loss of fitness through infanticide. Future work on the social ecology of arctic ground squirrels should consider infanticide as one of many factors affecting the complex interplay of these animals with each other, and with their environment.



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## APPENDIX 1

DIFFERENCES IN WEIGHT CHANGES AND  
THE ANNUAL CYCLE OF MALE AND FEMALE  
ARCTIC GROUND SQUIRRELS

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## ABSTRACT

Arctic ground squirrels (Spermophilus parryii) were studied for three summers near Haines Junction, Yukon Territory. Population characteristics and the behaviour of individual animals were monitored throughout the study. Ground squirrels entered hibernation in the order adult females, juvenile females, then males. Males emerged from hibernation before females. Males stored food in the autumn when conditions permitted, whereas females did not. Males emerged from hibernation having lost significantly less weight than females overwinter. Males lost weight during the mating period, whereas females did not. These data are interpreted in terms of the mating period which for males lasts for approximately three weeks, whereas for females it lasts for less than a day.



## INTRODUCTION

The primary tactic adopted by hibernating mammals for overwinter survival is to deposit large amounts of fat late in the active season, and to utilise this as a metabolic reserve through the hibernating period (Mrosovsky, 1971; Galster and Morrison, 1976). Such fat reserves may be supplemented by stored food substances such as seeds, but no data are available for ground squirrels on the relative importance of these two sources of energy. As much as half of a ground squirrel's energy budget during the hibernating period may be allocated to activity during the inter-torpor (i.e. active) phases (Wang, 1979). Thus stored foods could be an important supplement to stored fat.

As a consequence of the northern and high elevation environments in which they live, many hibernating sciurids tend to be subject to variable, and sometimes extreme, conditions in the spring (Morton and Sherman, 1978). This variability can affect the onset of emergence and breeding (Slade and Balph, 1974; Morton and Gallup, 1975; Michener, 1977, 1979a), and may prevent reproduction by at least some individuals altogether (Morton and Sherman, 1978).

In hibernating ground squirrels (genus Spermophilus), females tend to emerge after males (S. armatus, Slade and Balph, 1974; S. beldingi, Morton and Gallup, 1975; S. richardsonii, Michener, 1977; S. parryii, Green, 1977; S. lateralis, Bronson, 1980), breeding occurs almost immediately, much of the active season is devoted to the production of independent juveniles, and, although this is difficult to determine, males tend to enter hibernation before females (S. tridecemlineatus, McCarley,



1966; S. franklinii, Murie, 1973; S. richardsonii, Michener, 1977; although see Knopf and Balph, 1977). Autumn immergence may be affected as much by the condition of individual animals as by seasonal events (Michener, 1978, 1979a). Patterns of weight change have been monitored in many studies (e.g. S. lateralis, Skyrja and Clark, 1970; S. parryii, Green, 1977; S. richardsonii, Michener, 1978), but in few have the weights of the same individuals been monitored regularly through the season, or between seasons. Also, few data exist on food caching by hibernating sciurids, although there are occasional references to its occurrence, or absence (Gordon, 1943; Krog, 1954; Mayer and Roche, 1954; Morton, et. al., 1974; Yahner and Svendsen, 1978).

In this paper we show differences in the patterns of food storage, changes in weight, and entry into and emergence from hibernation, for male and female Arctic ground squirrels (Spermophilus parryii plesius)

#### METHODS AND STUDY AREA

Arctic ground squirrels were studied at an elevation of 600 m on a 60 ha area called Bear Creek flats located ten km west of Haines Junction, Yukon Territory (61°47'N; 137°40'W), and adjacent to Kluane National Park. The study area, described in detail elsewhere (McLean, in prep.), consisted of meadows interspersed among areas of willow (predominantly Salix glauca) with scattered stands of aspen (Populus tremuloides) and spruce (Picea mariana)





The area was visited from 28 April through 15 October, 1977, 16 April through 26 September, 1978, and 2 April through 8 July, 1979. The peak of mating was over on our arrival in 1977 and most animals had entered hibernation when we left; many males had emerged when we arrived in 1978, but we were present for the emergence of most females, most females but few males had entered hibernation when we left; we were present for the emergence of all animals in 1979. Most animals active in the area were live-trapped with National or Tomahawk box traps baited with peanut butter by 5 May, 1977, and 20 April, 1978, and we trapped animals as they appeared in 1979. Detailed observations of animals in two areas were undertaken once the mating period was underway and the entire study area was trapped once weekly through the rest of the season.

All animals were tagged with two individually numbered ear tags on first capture. Juveniles were captured as they emerged from natal burrows in the observation areas, and within one or two weeks of emergence in other areas.

## RESULTS

Arctic ground squirrels entered hibernation in the order: adult females, juvenile females, males. Adult females began to disappear from the observation areas in late July and the last adult females were trapped on 9 (1977) and 13 (1978) September. Juvenile females began



disappearing in late August and the last was captured on 1 October, 1977, (18 juvenile females were captured in the last week of trapping, 17 to 24 September, 1978). Some adult and juvenile males were still active at the time of the first major snowfall on 14 October, 1977. Those that did not enter hibernation at this time did so when temperatures dropped to  $-20^{\circ}\text{C}$  on 26 October (B. & G. Jeeves, Mile 1022 Alaska Hwy, Yukon, pers. comm.). The autumn was mild in 1978 and some squirrels remained active into November (Jeeves, op. cit.). Although males remained active into October, their mean weights peaked during September and a slight decline occurred during October (McLean, unpubl.). Thus we consider weights recorded for individual males after mid-September to be a maximum estimate of the weight at entry into hibernation.

In order to determine entry into hibernation quantitatively, we compared the last date of capture of individual animals that were subsequently trapped in a following year. Last capture dates were combined to give totals for bi-weekly intervals from mid-July onwards (Fig. 1), the earliest time at which animals could be considered to have entered hibernation. This ensured that animals that were lost in the fall due to factors such as predation or disease were not included, although it also excluded any animals for which a valid last capture date was obtained, but which died during the winter. Data in Figure 1 were compared using contingency table analysis, but because some values (particularly for adult males) were the minimum usually required for such analysis, we also made comparisons using Spearman's rank correlation coefficient (Table 1). Group differences for all data combined were highly signifi-





Figure 1: Last date trapped for individual Arctic ground squirrels that were also trapped in a subsequent season.

Data for autumn 1977 and autumn 1978 combined.

Mid September peaks for males would probably have shifted to the right if trapping had continued into October in 1978. Data after mid September for 1977 only.



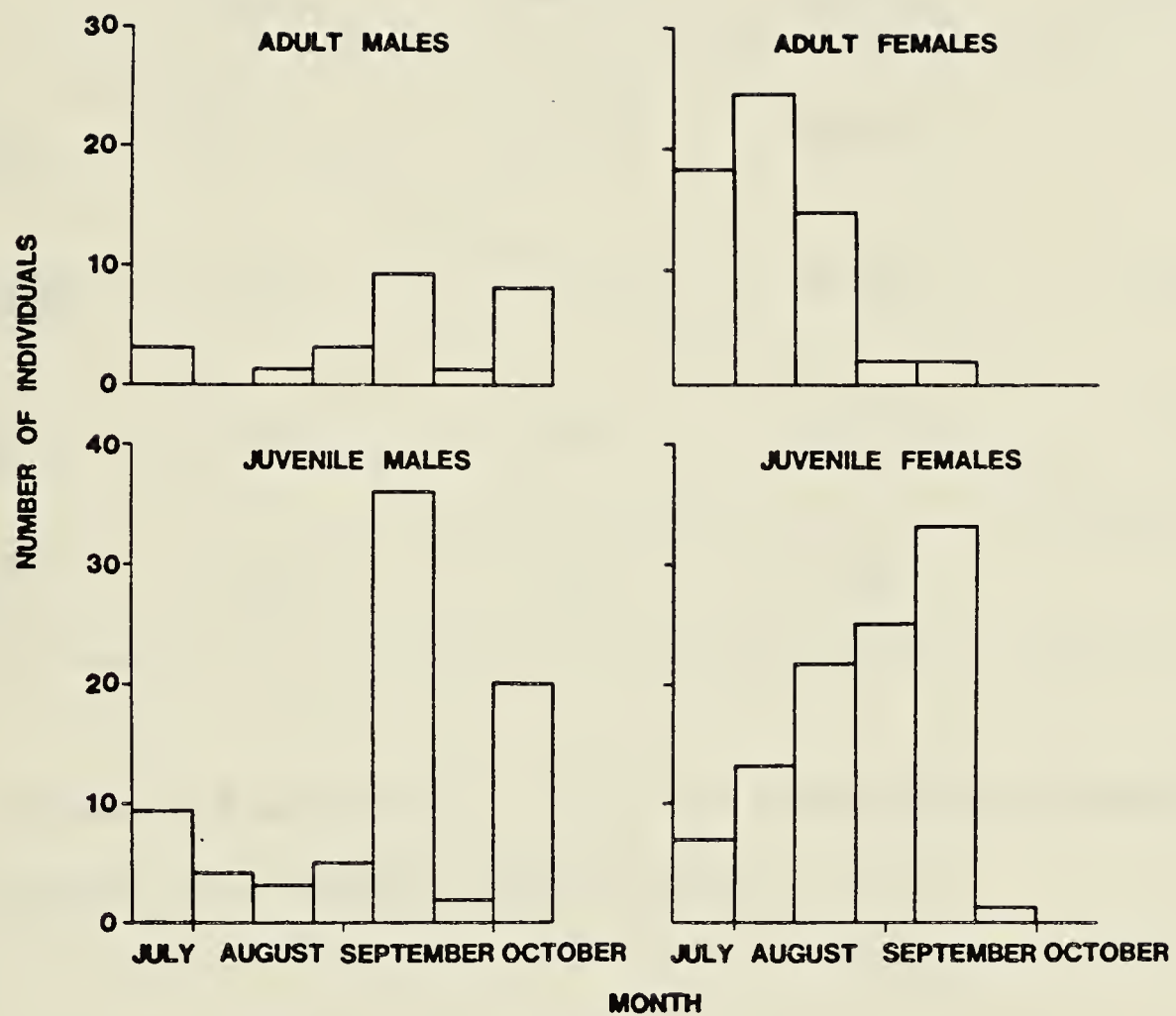




TABLE 1: Chi square values and Spearmans rank correlation coefficients for comparison of last date of capture for various age and sex classes of arctic ground squirrels (see Fig. 1).

	Adult females	Juvenile females	Adult males	Juvenile males
Adult females	$r_s$	51.46 <sup>+</sup>	54.46 <sup>+</sup>	76.95 <sup>+</sup>
Juvenile females	< 0.20		41.30 <sup>+</sup>	50.04 <sup>+</sup>
Adult males	< 0.20	< 0.20		2.92
Juvenile males	< 0.20	0.21	0.88 *	

Degrees of freedom for  $\chi^2 = 6$  in all cases except comparison of adult females with juvenile females where d.f. = 5.

Overall  $\chi^2_{18} = 146.70$  <sup>+</sup>

<sup>+</sup> Significantly different P < 0.001.  
\* Significantly correlated P < 0.05.



cant ( $\chi^2_{18} = 146.70$ ,  $P < 0.001$ ) indicating that differences in the distribution of last capture dates varied significantly between age and sex classes. Results of pairwise comparisons were similar for both analyses; last capture dates for adult and juvenile males were similar, and significantly later than for both female classes. Last capture dates for juvenile females were significantly later than for adult females, yet significantly earlier than for both male classes.

To further test this result, we compared the week of last capture of juvenile females and the week of last capture for the same individuals in the following year with similar dates obtained for known adults in both years. Nineteen juvenile females were last captured an average of  $3.53 \pm \text{s.e. } 0.80$  weeks earlier the following year (i.e. as yearlings entering their second winter of hibernation). Eight older females were last captured an average of  $0.25 \pm 1.05$  weeks earlier. This supports the above indication that adult females enter hibernation earlier than juvenile females. Similar data were not available for males because we did not remain on the study area late enough in 1978.

Males emerged from hibernation earlier than females in both 1978 and 1979. No ground squirrels emerged after 7 May in the observation areas in any year and it is used as an arbitrary cut off date in the following analysis. On 17 April, 1978, seven males and no females were trapped; by 20 April, nineteen males and six females had been trapped. This was not significantly different from an expected ratio of unity ( $\chi^2_1 = 3.63$ ,  $P > 0.05$ ) but was significantly different from the ratio of all males to all females (57:73) caught before 7 May ( $\chi^2_1 = 8.74$ ,  $P < 0.01$ , first





captures only used). In 1979, the first male was seen on 7 April, and sixteen males and one female were captured by 17 April. Thirty-eight males and nineteen females were captured by 22 April and this ratio was significantly different from the ratio of males to females (71:106) captured before 7 May ( $\chi^2_1 = 12.22$ ,  $P < 0.01$ ). These data indicate that males emerged earlier than females from hibernation by a factor of one to two weeks.

There was little indication that yearling animals of either sex emerged later than older animals. A few yearling males emerged late and were not sexually active but many of the dominant territorial males were yearlings. The emergence of yearling females was spread over a slightly longer period than that for older females, with some small yearling females not appearing until early May. As a result, first weights of females were only taken for older animals trapped before 30 (1978) and 29 (1979) April, and for yearling animals trapped before 7 (1978) and 6 (1979) May. These dates correspond to the ends of the weekly trapping programs. All females bred during this study.

Adult males and juvenile males lost significantly less weight than adult and juvenile females respectively during the 1977/78 winter (Table 2). All males combined lost significantly less weight than all females ( $P < 0.05$ , all cases, Mann Whitney U tests). Within sex differences were not significant. These data indicate that males lost less weight than females through the winter.

In 1979, males were trapped as they emerged from hibernation and they gained weight during the period before female emergence (Fig. 2).



TABLE 2: Loss of weight through the winter by individual male and female arctic ground squirrels trapped both in the autumn and the spring.

	1977/78	1978/79	
	Oct to 23 Apr	17-24 Sept to 15 Apr	
<u>Adult males</u>			
$\bar{X} \pm \text{s.e. (gm)}$	61.4 $\pm$ 29.87	144.4 $\pm$ 24.90	
$\bar{X} \pm \text{s.e. (% loss)}$	8.2 $\pm$ 4.03	18.3 $\pm$ 2.79	
N	7	8	
<u>Juvenile males</u>			
$\bar{X} \pm \text{s.e. (gm)}$	114.0 $\pm$ 16.73	163.3 $\pm$ 32.14	
$\bar{X} \pm \text{s.e. (% loss)}$	17.1 $\pm$ 2.56	22.0 $\pm$ 3.39	
N	10	6	
	1977/78	1978/79	Total
<u>Adult females</u>			
$\bar{X} \pm \text{s.e. (gm)}$	208.9 $\pm$ 26.60	205.3 $\pm$ 17.55	206.4 $\pm$ 14.39
$\bar{X} \pm \text{s.e. (% loss)}$	32.7 $\pm$ 3.72	31.2 $\pm$ 2.50	31.7 $\pm$ 2.04
N	9	20	29
<u>Juvenile females</u>			
$\bar{X} \pm \text{s.e. (gm)}$	157.4 $\pm$ 13.69	134.6 $\pm$ 8.02	142.0 $\pm$ 7.09
$\bar{X} \pm \text{s.e. (% loss)}$	29.2 $\pm$ 2.32	25.6 $\pm$ 1.47	26.8 $\pm$ 1.26
N	17	35	52



This gain suggests that the values used in the above analysis for 1977/78 overwinter weight loss by males were underestimates of the actual weight lost (spring weights were of males caught as females were beginning to emerge). However, increasing the above estimated weight loss of 61.4 gms by 31.3 gms (the mean weight gain of twelve males during the two weeks prior to emergence of females in 1979) increases the percent loss during the 1977/78 winter to 12-13%, still considerably less than the 32.7% recorded for adult females. The gain in weight by adult males in the early spring was followed by a precipitous weight loss during the mating period (Fig. 2). Weights stabilised in mid-May once mating was over. Females gained weight immediately after emerging from hibernation and continued to do so until giving birth during the second two weeks of May (Fig. 2). Mean  $\pm$  s.e. weight loss at birth of twenty-four females was  $61.3 \pm 4.39$  gm (maximum of four days between weighings).

Equivalent data for overwinter weight loss for 1978/79 were available for females, but not for males, because trapping ended before the males began to enter hibernation. Since accurate emergence weights for males were available in 1979, we obtained a measure of overwinter weight loss by subtracting weights of males trapped before 16 April from weights of the same individuals trapped during the week 18 to 24 September, 1978 (the last week of trapping). These values are maximum estimates of loss since weights tended to decrease in October (above). Mean losses by adult and juvenile males were 18.3% and 22.0% respectively, and by adult and juvenile females were 31.2% and 25.6% respectively (Table 2). These differences were significant for adults ( $P < 0.05$ , Mann Whitney U test) but not for juveniles ( $P > 0.05$ ). All males combined lost significantly



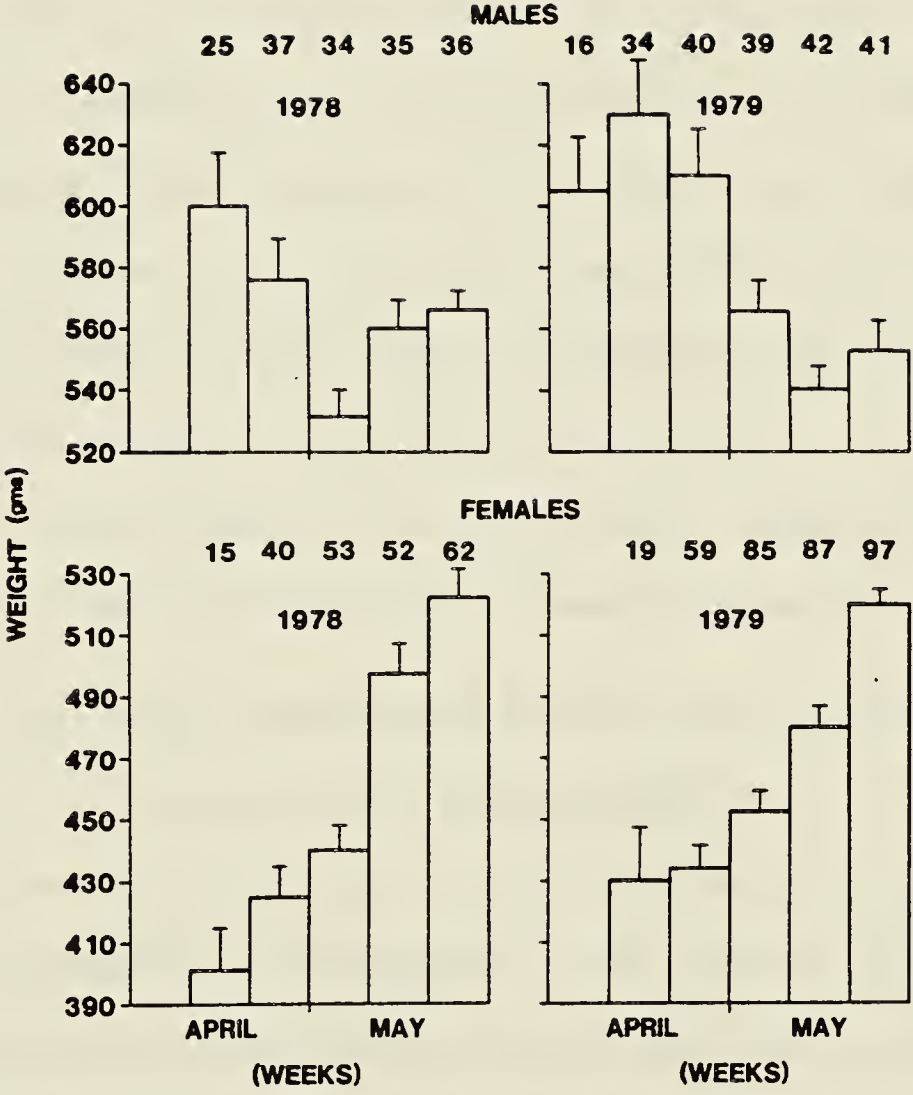




Figure 2: Weight changes of adult male and female Arctic ground squirrels during the springs of 1978 and 1979.

Bar gives mean + s.e.

Number of animals included in calculation of mean indicated above bar.





less weight than all females combined ( $P < 0.05$ ). As with the 1977/78 data, age differences within each sex were not significant.

Arctic ground squirrels spent considerable time collecting various materials (seeds, green and dried leaves, flowers, berries, and mushrooms) and carrying them to burrows. Dried grasses were carried in the mouth and were probably used for nests and bedding (c.f. Steiner, 1975); other materials were carried in the cheek pouches. No attempt was made to record the numbers of animals seen collecting material in cheek pouches; however it was apparent from our observations that females collected during lactation (late May and June) before they entered natal burrows, presumably to feed litters. Males spent considerable time collecting seeds during July and August and tended to spend only one or two minutes underground when carrying these to a burrow system. Females were only very rarely observed making collections in cheek pouches after June.

Animals with full cheek pouches were often trapped (Table 3). They invariably expelled collected material during handling so that identification of both the sex of the collector and the contents of the pouches was possible. As indicated by observations, most females with full cheek pouches were trapped during June, whereas males with full cheek pouches were trapped rarely before July. Although no attempt was made to quantify the relative proportions of materials collected, female collections consisted primarily of flowers and leaves, whereas male collections were predominantly of seeds.

Two factors affected the collection of these data:





TABLE 3: Numbers of arctic ground squirrels captured with full cheek pouches and material collected from those animals during 1977 and 1978.

	Adult males	Juvenile males	Adult females	Juvenile females	Total	Seeds	Flowers Leaves	Other	Total
April/May	1	-	-	-	1	-	-	1	1
June	3	-	5	-	8	2*	6	1	9
July	10	-	1	1	12	9	2	3	14
August/September	4	21	-	1	26	19	8	-	27
TOTAL	18	20	6	2	47 <sup>+</sup>	30	16	5	51 <sup>+</sup>

\* Both these were males.

+ Totals different due to some cheek pouch samples containing more than one type of material.



1. Because females were entering hibernation during August and September, the numbers captured decreased through this period. However, females were more abundant in the population than males (McLean, unpubl.) so that it was not until August that the numbers of females captured weekly fell below that of males. We compared the number of captures of males to captures of females (1252:1024) during July, August, and September of 1977 and 1978 with the equivalent ratio of animals captured with full cheek pouches (34:3). These were significantly different ( $\chi^2_1 = 20.07, P < 0.01$ ) indicating that the greater number of males than females captured with full cheek pouches in the later part of the season was not an artefact of capture frequency.
2. Almost no rain fell on the study area from snow melt until early August in 1978 (Fig. 3). As a result most of the vegetation in the meadows had turned brown by mid-July, and the seed crop, which in 1977 had been extensively harvested by males, failed almost completely. Very few animals were seen making cheek pouch collections, and only one was trapped with full cheek pouches after June, 1978.

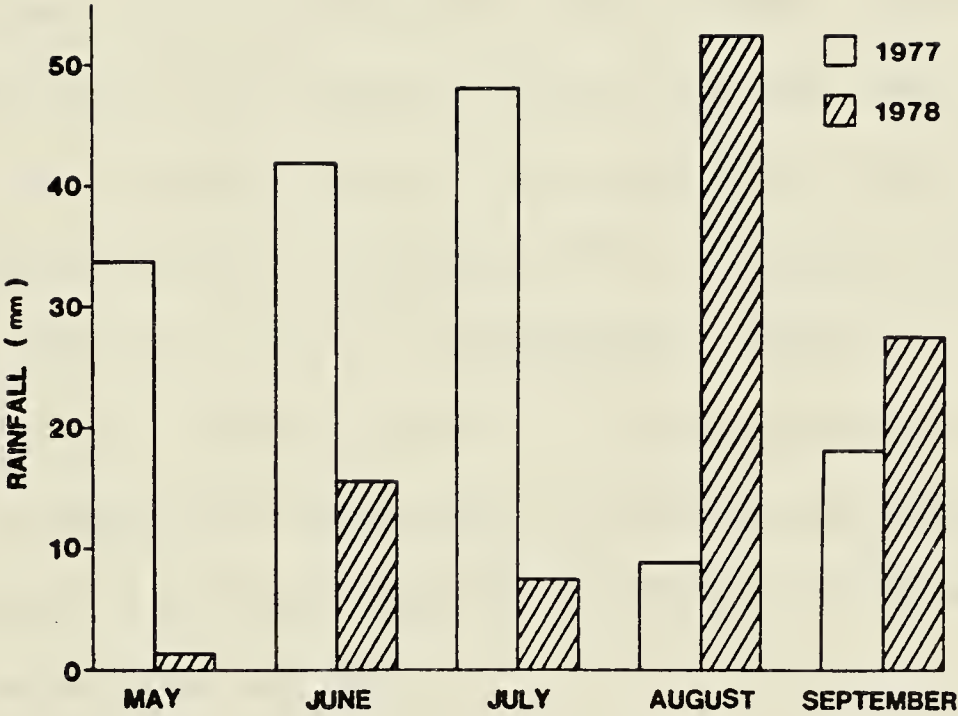
These data suggest that, conditions permitting, males spend more time than females making collections of foods suitable for storage. The short time spent underground by males who emptied their cheek pouches further suggests that collected material was stored.





Figure 3:      Rainfall on Bear Creek flats, Yukon Territory, during  
1977 and 1978.







## DISCUSSION

Immediately after emergence in the spring, female arctic ground squirrels are mated by one, or perhaps several, males (see also Sherman, 1980b), after which they gain sustenance both for themselves and for the developing litter. Males attempt to copulate with females as well as prevent other males from gaining access to those females (Carl, 1971; McLean, in prep.). Female arctic ground squirrels probably mate on their first day of estrus, and at most are in estrus for one to two days (Unpubl. data; see also Murie and McLean, 1980). However, the mating period, which is of primary interest to males, lasts for up to three weeks. Once mating is over, females may have a higher energy drain than males (Galster and Morrison, 1976), particularly if males do not behave paternally, as in S. richardsonii (Michener, 1979b) and S. beldingi (Sherman, 1980a), but not in S. parryii (McLean, 1979; and in prep.). The possibility that males and females may follow different tactics in coping with these different behavioural and physiological factors has rarely been addressed.

Greater overwinter weight loss by female arctic ground squirrels may be attributed to two factors: i) their longer time (one to two months) in hibernation, and ii) their lack of food stores. That males actually use food stores during the winter was suggested by the greater overwinter weight loss recorded for 1978/79 when food stores were not available, than in 1977/78 when they were. Unfortunately, the data are not strictly comparable. By entering hibernation early, females presumably avoid above-ground predators (Slade and Balph, 1974) and may avoid a period when



the vegetation is of poor quality (Bliss, 1962; Scotter, 1972). Males, by remaining active, may maintain their pre-hibernation fat reserves until later in the season and also amass greater food stores. Males also may enhance their access to females in the spring by territorial behaviour in the fall (Carl, 1971; Green, 1977).

Suitable physiological data for comparison with the present study are difficult to obtain. Loss of weight by males in the spring has been reported in various species (e.g. S. richardsonii, Zegers and Williams, 1977; S. armatus, Knopf and Balph, 1977); however, in some of these species females also lost weight. Differential weight loss between the sexes over winter and in the spring has been reported for arctic ground squirrels (Mayer and Roche, 1954; Green, 1977) yet males have been found to lose less fat than females before the end of June (Kiell and Miller, 1980). A weight loss during the "reproductive period" was reported by Galster and Morrison (1976) for female arctic ground squirrels, but their samples were small and weights were of laboratory animals.

In addition to the above factors, male arctic ground squirrels are involved in large numbers of interactions, sustain considerable wounding, and show different activity budgets than females during the mating period (Carl, 1971; Green, 1977; McLean, in prep.). Vegetation is of poor quality in the spring in northern ecosystems (Billings and Mooney, 1968) and high energy food stores (seeds) and metabolic reserves could presumably allow males to devote more time to sexual activity during this critical period. Heavier animals could be more dominant in interactions over estrus females, and food stores left over from the winter may serve





to attract females into a male's area (we consider this latter hypothesis unlikely). The data presented here show intersexual differences in the tactics adopted by males and females. Although some differences appear to be unique to arctic ground squirrels, detailed analysis of the patterns shown by individuals in other species may show similar trends.



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Appendix 2: Weights of arctic ground squirrels on Bear Creek flats, Yukon Territory, during 1977, 1978, and 1979.

Year	Week of trapping (week ending)		Adult males			Adult females			Juvenile males			Juvenile females		
			Mean weight (gm)	s.e.	N	Mean weight (gm)	s.e.	N	Mean weight (gm)	s.e.	N	Mean weight (gm)	s.e.	N
1977	May	3	501.6	21.11	14	395.6	13.43	21						
		10	520.6	14.21	16	427.7	13.30	32						
		17	506.4	15.97	16	471.4	11.61	36						
		24	538.8	19.93	13	477.4	9.52	35						
		31	556.4	15.14	11	477.4	8.30	28						
	June	7	567.2	15.10	10	490.7	7.78	38						
		14	598.7	15.53	15	504.7	8.35	37						
		21	623.8	-	4	497.9	13.96	16	121.5	5.64	24	108.1	4.52	27
		28	611.7	18.16	9	512.3	13.39	15	168.7	7.11	27	152.4	7.45	27
	July	5	575.7	12.02	7	491.1	11.54	18	226.9	11.94	19	208.2	10.79	24
		12	579.0	27.68	5	503.6	10.41	20	247.9	20.86	20	290.5	10.60	25
		19	578.6	16.39	7	524.6	17.23	13	378.2	20.75	21	344.3	12.57	25
		26	616.1	17.09	9	575.2	18.87	11	417.8	21.32	16	390.0	8.45	15
	August	2	621.4	16.58	11	627.8	25.40	9	515.3	13.99	19	454.8	11.56	18
		9	647.7	17.66	13	588.0	20.66	10	528.6	9.28	32	463.6	8.72	25
		16	654.5	19.56	10	571.0	30.14	5	572.3	8.57	24	511.6	9.75	16
		23	672.9	17.66	12	570.0	-	1	597.0	11.75	25	515.0	12.92	12
		30	688.1	16.83	12	585.0	-	1	592.2	10.09	30	543.4	9.49	16
	September	6	699.5	18.32	11	597.5	-	2	619.3	10.43	28	551.0	12.18	10
		13	700.5	19.79	11	550.0	-	1	646.7	9.49	30	556.0	11.08	10
		20	705.5	17.91	10			0	652.8	11.82	28	557.5	20.53	8
		27	695.0	19.52	10			0	650.0	12.13	28	472.5	-	2
	October	4	685.5	20.22	11			0	650.7	15.81	29	465.0	-	1
		11	707.5	21.23	8			0	640.8	15.95	26			0
		18	665.0	-	2			0	630.0	23.93	14			0
1978	April	23	600.1	17.50	25	401.3	14.43	15						
		30	575.9	12.76	37	423.7	11.26	40						
	May	7	531.3	9.66	34	440.4	8.15	53						
		14	559.2	7.94	35	498.1	9.18	52						
		21	565.1	7.48	36	523.3	8.41	62						
		28	590.7	7.62	34	516.0	6.01	58						
	June	4	611.8	8.51	34	512.9	6.46	64						
		11	631.7	9.46	27	540.7	5.39	72						
		18	639.5	7.36	30	542.5	4.97	61	120.1	3.24	10	125.1	8.36	8
		25	647.3	7.86	30	545.5	5.42	74	184.5	5.09	52	173.2	5.05	60
	July	2	640.2	10.86	23	517.4	5.36	60	245.7	9.87	48	228.5	6.55	51
		9	665.0	14.21	21	512.6	6.83	53	302.4	8.97	56	272.2	7.62	63
		16	645.2	13.32	23	555.1	8.03	39	367.7	8.39	61	352.4	6.47	73
		23	669.7	12.47	26	571.9	8.57	39	423.1	11.84	49	385.7	8.06	50
	August	30	695.6	13.57	26	622.8	11.39	25	495.8	11.86	39	421.5	9.23	42
		6	745.7	15.67	23	644.2	13.18	24	515.3	13.58	39	458.4	9.87	46
		13	729.7	16.54	19	627.3	17.08	15	525.6	13.45	44	461.8	8.94	48
		20	751.0	20.36	15	656.3	10.08	8	555.8	16.12	31	474.9	10.38	39
		27	765.6	17.07	18	628.6	17.77	9	582.0	11.72	51	520.4	8.47	39
	September	3	790.9	20.84	16	610.0	-	3	607.7	13.27	41	510.2	11.40	31
		10	808.6	16.60	21	650.0	-	1	624.6	15.09	34	526.3	11.74	32
		17	801.2	17.74	21	615.0	-	1	634.0	11.99	42	525.5	10.86	28
		24	800.2	19.28	17			0	637.0	14.15	31	510.3	14.54	18
1979	April	15	604.1	18.70	16	345.0	-	1						
		22	634.9	13.12	34	429.4	17.61	19						
		29	614.8	9.90	40	433.8	7.69	59						
	May	6	564.5	11.42	39	451.5	7.42	85						
		13	539.3	8.72	42	479.8	6.97	87						
		20	552.4	8.48	41	519.5	5.42	97						
		27	581.8	8.46	29	510.2	5.14	86						
	June	3	590.8	6.72	36	501.6	4.47	90						
		10	620.4	7.67	34	514.7	5.69	74						
		17	617.5	9.09	48	513.2	4.33	91						
		24*	650.0	-	2	525.5	12.42	11						
	July	1	641.4	9.33	33	498.4	3.95	96						
		8*	652.5	-	4	540.0	-	3						

Number of traps set was increased from approximately 120 per week in 1977 to approximately 200 per week in 1978 and 1979.

\* Trapping curtailed during these weeks to allow increased observation.



### Appendix 3

#### PLUGGING OF NEST BURROWS BY FEMALE *SPERMOPHILUS COLUMBIANUS*

Columbian ground squirrels (*Spermophilus columbianus*) are known to plug hibernaculum burrows, and several ground squirrel species (*S. tridecemlineatus*, *S. mexicanus*) plug commonly used burrows on a daily basis (MacClintock, 1970). There are, however, no records of ground squirrels plugging some holes while using others, or of squirrels plugging holes that are to be used at a later date, although Linsdale (1946:339) suspected ground squirrels of plugging nest holes at parturition. Observations on part of a large (approximately 1,000 animals) colony of *S. columbianus* in southwestern Alberta from April until June 1976, indicated that the normally conspicuous burrow systems of these animals were not used for rearing young. Litters were generally raised in small inconspicuous burrows located on the periphery of the major burrow systems. The behavior of females when near these burrows appeared to maintain their relative inconspicuousness.





Nine adult males, including one Richardson's ground squirrel (*S. richardsonii*), 18 adult females, and two male yearlings, were resident in the 1.5 ha area during the observation period. The *S. richardsonii* left the area in early May after breeding was completed, and one female died (road kill) on 5 June. Ten of the females brought up young (the dead female did not appear to be pregnant). Although the *S. richardsonii* managed several copulations, none of the young appeared to be hybrids.

Behavior associated with the gathering of nest material was as described in Betts (1976). All animals gathered nest material throughout the season, but in early May females began to take material to very small holes that were opened from underground (there was no loose earth to indicate the position of the hole). These animals continued to emerge each morning from their usual burrow systems, which were associated with large mounds, and also continued to carry nest material to these systems. Carrying nest material to the small holes was usually continuous for several hours and lasted for 1 to 3 days, whereas carrying nest material to other holes generally lasted for less than 1 h and occurred sporadically throughout the season.

Of 38 holes to which females carried nest material, young subsequently emerged from eight (the nest holes of two females were not found until the young emerged), females emerged in the morning from 18 (includes holes used by females before they gave birth), and 12 were not used for morning emergence or as nest holes. All eight nest holes were plugged with earth within a day of the last observation of the animal carrying nest material, and were left closed for up to 4 days, when either the same hole was reopened, or a new one was opened within 1 m. The squirrel either gave birth at this time, or carried more nest material to the hole and replugged it. In most cases, the hole was so effectively concealed after plugging that it could not be located without reference to a previously placed marker. Of the 12 holes that were filled with nest material and not subsequently used, five were filled by females that gave birth in a different hole (three were plugged), and seven were filled by females that did not give birth (four were plugged). It appeared that those females that did not give birth were preparing nest chambers in the same way as those that did, suggesting that they were pregnant at this stage. I excavated a hole located just off the study area, which was filled and plugged in the same manner as nest holes. The end of the plug was not reached at a depth of 50 cm, and open burrow was not found, suggesting that the plugs are relatively long.

The mean distance that nest material was carried to the holes used for morning emergence (mean  $\pm$  SD, carrying distance =  $8.0 \pm 5.01$  m,  $N = 17$ ) was significantly less than the distances that nest material was carried to the holes classed as either holes used for rearing young ( $14.3 \pm 3.68$  m,  $N = 10$ ), or small inconspicuous holes not used for morning emergence or for parturition ( $14.1 \pm 8.19$ ,  $N = 14$ ) (based on mean carrying distances for 1 day;  $P < 0.01$ ; one way ANOVA, Duncan's multiple range test). This difference suggests either that nest material may not have been available near nest holes and nonemergence holes, or that females were behaving in a way that would not draw attention to the small holes. I could not detect major differences in the abundance of nest material around any of the hole types.

Just prior to giving birth, females began emerging in the morning from the small holes from which the young subsequently emerged. Some of these holes were plugged each night and opened in the morning for up to 2 weeks. In two instances the hole was also plugged during the day. The juveniles emerged approximately 25 days after birth, and within 1 to 3 days began emerging in the morning from the females' usual burrow systems. It appeared that nest holes, although located near the periphery of major burrow systems, were separated (by underground plugs perhaps) until the juveniles emerged.

Because Columbian ground squirrels did not plug nest holes consistently when the young were developing and holes were plugged prior to birth of young, it seems unlikely that the plugs were related to protection from predators and weather. In addition, because I was able to determine the location of nest holes, it seems unlikely that cryptic behavior during gathering of nest material, and plugging, concealed them from resident conspecifics. However, aggressive, wide-ranging adult males that were seen only sporadically in any part of the colony would be less likely to find well-hidden holes, would have a low probability of being the parent of young in the area, and could possibly increase the future survival of their own young by killing others (Hamilton, 1970). No intraspecific predation on juveniles has been observed during 3 years of study on the area (J. O. Murie, personal communication), although one instance of an adult male killing a yearling was recorded in 1976 (A. Wroot, personal communication). Steiner (1972) reported "marauding males" attacking juveniles in both Columbian and Arctic (*S. parryi*) ground



May 1978

## GENERAL NOTES

439

squirrels, and Sherman (1976) has found intraspecific predation to be a strong selection force in the social system of Belding's ground squirrel (*S. beldingi*). Thus cryptic behavior and plugs could be responses to predation by nonresident conspecifics.

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## Appendix 4

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## COPULATORY PLUGS IN GROUND SQUIRRELS

Copulatory plugs, coagula formed in the vaginae of females after copulation and male ejaculation, occur in a wide variety of mammals, but are best known in the rodents (Hartung, 1976). Among sciurids, plugs are reported for gray squirrels, *Sciurus carolinensis*, and white-tailed prairie dogs, *Cynomys leucurus* (Asdell, 1964), thirteen-lined ground squirrels, *Spermophilus tridecemlineatus* (Foster, 1934), and Beechey's ground squirrel, *S. beecheyi* (Tomich, 1962). All these reports come from laboratory studies, possibly because field researchers have not inspected females at the right time or in enough detail to notice plugs.

During a laboratory study of vaginal cell cycles through estrus, one female Columbian ground squirrel (*Spermophilus columbianus*, C.g.s.) mated and a copulatory plug was found. Subsequently, during regular mark-and-release trapping of Columbian and Arctic (*Spermophilus parryi*, A.g.s.) ground squirrels in 1977 and 1978, we made vaginal smears from females during the breeding period (late April to mid-May) and checked systematically for copulatory plugs. C.g.s. were trapped in southwestern Alberta (50°38'N, 114°38'W) about 32 km W Turner Valley, elev. 1,500 m, where studies of social behavior (Murie and Harris, 1978) and demography are in progress. A.g.s. were studied 9 km N Haines Junction, Yukon Territory (60°37'N, 137°40'W), elev. 600 m.

Vaginal smears were taken from 28 C.g.s. and 35 A.g.s. during 1977, and 28 C.g.s. and 23 A.g.s. during 1978; three or more (up to 10) smears were taken on consecutive or alternate days from 34 C.g.s. and 23 A.g.s. during the two seasons. Smears were obtained by rinsing the vagina with a pipette and 0.1 to 0.2 ml of saline, drying on a clean microscope slide, and staining with Shorr's (1941) stain.

We observed copulatory plugs in 16 C.g.s. and 8 A.g.s. Eleven (9 from C.g.s.) of the 24 plugs were anchored deep (about 1.5 cm) in the vagina and were not readily detectable until a pipette was inserted to obtain a smear. The other plugs were visible; seven (3 from C.g.s.) were very loose and almost falling out of the vagina, and six (4 from C.g.s.) adhered strongly to the vaginal wall and resisted attempts to remove them. Three of the plugs in each species were very hard, yellowish, and crystalline on the outer surface. The others, although relatively hard, were white and rubbery. Three plugs from C.g.s. that were partially extruded and loose were removed. Lengths were 14, 13, and 15 mm; widths in two perpendicular planes at the external end were 11 by 6 mm, 7 by 4 mm, and 5 by 3 mm, respectively. All three tapered slightly towards the inner end.

We have little information on how soon after copulation a plug forms. These ground squirrels rarely copulate above ground, but we have been able to estimate the time of breeding for a few individuals from male and female behavior. Vaginal smears were obtained from three C.g.s. females 3 to 4 h after a presumed copulation underground, and although plugs were not evident, numerous sperm were present. The following day, 18 to 20 h later, two had loose external plugs and one had a deep plug. It is possible that deep, soft plugs had formed in these females at the time of the first inspection but were not detected by probing. In a number of rodents copulatory plugs form within 30 min (Hartung and Dewsbury, 1978). If plugs do form as rapidly in C.g.s., we were unable to detect them by inspection of the live animal.

Five other C.g.s. females and two A.g.s. females were examined the day after a deep plug was found. Two C.g.s. and both A.g.s. females had lost plugs, two had loose plugs 17 and 19 h later, and one still had a deep plug 19 h later. Four C.g.s. females that had abundant sperm in their vaginal smears on one day did not have visible plugs the next day, 20 to 24 h later, or the day after, 44 to 50 h later. Either plugs did not form in these individuals or they were lost before capture on the following day. The introduction of saline could have affected plug formation, although plugs were found in three other females from which smears with abundant sperm had been taken previously.

Our data suggest that the length of time plugs persist is variable. The minimum durations of plugs in three C.g.s. females were 17 to 19 h. Foster (1934) implied that plugs in *S. tridecemlineatus* persisted for 3 days, a longer period than our data suggest for Columbian or Arctic ground squirrels. However, the duration of plugs in our animals appeared to be roughly similar to values reported for other rodents. Plugs in laboratory mice usually fall out after 18 to 24 h, but may persist for 2 days (Parkes, 1926). In guinea pigs (*Cavia porcellus*) "... the plug remains in the vagina for as long as 18 hours" (Martan and Shepherd, 1976).





Although we have no data directly related to the function of copulatory plugs in these ground squirrels, a role in reducing the likelihood of subsequent fertilization by another male, as documented for guinea pigs by Martan and Shepherd (1976), deserves investigation. Many of the plugs we found completely filled the vagina and adhered tightly to the vaginal walls; such plugs might block copulation or prevent the passage of sperm into the uterus. In addition, our observations of the social system of Columbian and Arctic ground squirrels during the breeding period indicate that males attempt to gain access to estrous females both within and outside their own territories. Territorial behavior by male C.g.s. during the breeding season has been interpreted as advantageous for increasing the likelihood of breeding with females in the area (Murie and Harris, 1978), and similar observations for A.g.s. (Carl, 1971; Green, 1977) suggest the same conclusion. If plugs served to prevent or reduce successful copulations by other males, this would free the male from protection of his investment in a particular female after copulation had occurred and allow him to search immediately for other receptive females. Hence selection pressure on males could exist that favored the deposition of a plug.

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